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Morphogenesis in Dictyostelium[1]

R. A. HARPER

(WITH PLATES 6–8)

INTRODUCTION

The development of a plant from the germ cell, spore or egg, to maturity is generally characterized broadly as a process of growth and differentiation; or speaking in even more general terms, growth is made to include differentiation. Considering the matter more analytically, there is still much confusion in the technical literature and in the definitions of the textbooks as to the relative significance and the interrelations, of cell growth, multiplication or census growth, histogenetic cell differentiation, and the morphogenetic processes by which the specific form and types of symmetry of the mature metaphytic plant are produced. This is in a way natural enough, since in most plants all these processes go on more or less simultaneously and the specific significance and the functions of each are apparently inextricably interwoven with those of the others.

That all of these so-called growth processes are essentially cell phenomena has been widely recognized since the second quarter of the last century, when the cell theory was given its present-day form by the work and writings of Von Mohl, Meyen and others.

Certain simple types of slime moulds present the phenomena of cell growth, cell reproduction and morphogenesis in, so to speak, dissected form and for such cases at least afford a very direct answer to De Bary's old question as to whether the plant builds cells or cells build the plant. I have elsewhere described (1918) the processes of morphogenesis in certain coenobic algae,

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such as *Hydrodictyon*, *Gonium* and *Pediastrum*, in terms of the interrelations of free and independent cell units. The Acrasieae present a further phase of these problems in that their completed forms in the higher types of the group are erect and tree-like in their habit, with at least an approach to metameric and radial symmetry in their organization.

Olive, in his very thorough study of the group (1902) brought together convincing evidence that we have in them a very complete evolutionary series so far as form is concerned from such simple cushion-shaped masses as *Copromyxa* to the branching pine-tree-like forms of *Polysphondylium*, with its evenly tapering stem and whorls of progressively shorter branches.

I am here presenting, in microphotographs, the more essential stages in the development of *Dictyostelium mucoroides*, a form which only occasionally branches, but produces a symmetrically tapering stalk with a mass of spores at the apex, simulating the sporangiophore and sporange of *Mucor* as its name implies. The difficulties in photographing such material are very great, and the prints I have obtained leave much to be desired. The drawings of Zopf, Brefeld, and especially of Olive, show all the essential morphological structures and the method of their development. I have, however, thought it worth while in this case, as in the case of the coenobic algae, which I have studied from the same standpoint, to present the data in photographic form so that the measurements of size and the general symmetry relations may be shown free from any suspicion of interpretative bias. I have not attempted to free the surroundings of the plants photographed from extraneous material such as spores, minute fragments of dung which do not readily filter out of the decoction, etc. Bacteria are regularly present in these dung cultures without, however, ordinarily interfering with the apparently normal development of the *Dictyostelium*. The cultures were grown at ordinary room temperature and I am leaving also for future experimental study the effect of varying other environmental factors, such as moisture and food supply, chemical stimulation, etc.

It is to be noted also that the photographs are all, except where specifically noted, of material in the living condition. The amoebae in the creeping stages are slowly changing their form and position. It is impossible, of course, in the case of such

transparent bodies, to get photographs by instantaneous exposures. The photographs of creeping amoebae (PLATE 1, FIGS. 7–10, PLATE 2, FIGS. 17–23) were obtained by exposures of from five to fifteen seconds.

There has been wide disagreement in the use of morphological terms for the spore-bearing structures in the Acrasieae. Brefeld (1869) calls the spore-bearing organs sporanges and stalks. Zopf calls them sori and sorophores. Thaxter calls the similarly formed structures in the Myxobacteriaceae cysts and cystophores. The term cyst has been used very loosely. There is no question that it should be retained for those more or less transitory dormant stages of interrupted life activity which may intervene at any period in the life cycle and in which the organism encloses itself in a thick sheath.

Brefeld reports that encystment of the myxamoebae may occur at any stage in the development of the culture. He describes the process and the germination of the cysts quite fully but was unable to determine the conditions which bring it about. Olive states that encystment is brought about by slow drying. Zopf says that microcysts are formed under unfavorable nutritive conditions.

The use of the term cyst in the literature of the protozoa is even more confused by the fact that the term has been used for stages in which sexual reproductive processes are involved. This literature has been recently summarized by Kater and Burroughs (1926). It seems clear, however, that encystment is not in *Dictyostelium* a recurrent phenomenon in the life cycle in the same sense that the spore-bearing structures are, and if the term cyst is to be retained for the non-cyclic dormant stage, we should not use the same term for the spore-bearing structures. The term sorus, used by Zopf, is also variously and loosely used in mycological terminology. I shall use it for the spore mass to avoid the danger of confusion involved in the use of the term cyst. The stalk is then the sorophore, and I shall call the entire spore-bearing structure the sorocarp as such a term is much-needed in the description of the morphogenetic processes with which we are concerned. The amoebae for clearness should certainly be distinguished as myxamoebae, though convenience may lead to occasional abbreviation of the term. There are certainly adequate grounds for distinguishing these fruiting

structures, which are formed primarily by the morphogenetic aggregation of free cell units, from spore-bearing structures such as those of the mycelial fungi which are formed by the combined and simultaneous processes of growth and cell, or at least nuclear, multiplication. The latter are regularly regarded as growth forms. These more special types may be distinguished as aggregation forms, or by an extension of its current significance, morphallactic forms. With them should be included also those coenobic algae whose colonies are formed by aggregation of free swarming zoöspores. The view that the Acrasieae are primitive slime moulds seems to me to be supported by abundant evidence, and while in the latter the development of a true plasmodium, with its extended period of growth and nuclear division, tends to break down the limits of the category, in my opinion they also may be classed as aggregation forms.

STRUCTURE OF THE SOROCARP

Dictyostelium, as noted, has an easily recognized resemblance to a *Mucor*. I shall describe first the general facts as to the range in form, size and proportions of the *Dictyostelia* and then take up the data as to their life history and form development. The general form and proportions of an average specimen as grown in a hanging drop of dung decoction is shown in FIGURE 1. The outlines of the figure are by no means sharp. It is practically impossible to photograph these minute plants either on their natural substrata or as they grow erect in moist chambers. The working distance of the lenses is far too short.

It was early found, however, that when grown in hanging drops, the myxamoebae build the stipe downward only a short distance and then curve out horizontally. This is not in agreement with Brefeld's statement that the sorocarps grow out at right angles to the substratum, no matter how the latter is oriented. With the use of the very low magnifications given by the microplanars, it is possible to get figures appearing more or less as if the whole sorocarp were in one plane. The rather bulbous base is rather over emphasized in density, but the taper of the sorophore and the ratio of the diameter of the spore mass to the height of the whole plant are not seriously misrepresented.

The sorocarps shown in FIGURES 1 to 6 were photographed in this way. They were chosen to represent the wide range in

size and proportions which *Dictyostelium* shows. Its range of variability in these respects is certainly of the same general order as is found in other fungi and in the higher plants. The ratio of height to diameter of sorus in the plant shown in FIGURE 1 is about 10 to 1; the corresponding ratio in the plant shown in FIGURE 3 is about 2.3 to 1. In the two sorocarps in FIGURE 2 it is about 8 to 1.

These variations in size and proportions are doubtless due largely to environmental conditions, as in the higher plants, but as will be noted, there are certain problems in connection with what we call normal size in a species which can be studied experimentally to especial advantage in these forms.

In FIGURE 2, two small plants are shown which were growing rather close together in the culture and whose sorophores and sori lie nearly enough in the same plane so that they both appear in the photograph. The two sorocarps not only curve in a vertical plane by negative geotropism, but also in the horizontal plane, both bending in about the same direction to the left. The proportions of height to diameter of sorus in these two plants are about the same (8 to 1) though the sorocarps are quite unequal in size.

All five of the sorocarps (FIGS. 1 to 5) were growing scattered in hanging drop cultures, the bases of the sorophores attached to the microscope slide and immersed in the dung decoction. It is very common in hanging drop cultures to find the sorocarps at the margin of the drop as is shown in the case of those sorocarps photographed in successive stages of development and shown in FIGURES 18–21. In what are perhaps the most typical sorocarps, the sorus is globular, no matter from what angle it is viewed. Its form would thus seem to be the expression of simple surface tension relations. It is to be remembered, however, that at no time in its development, is it a continuous mass of protoplasm, much less a homogeneous liquid. Throughout its development it contains the upper portion of the sorophore, which extends as a relatively solid axis from its basal to its apical pole. In its earlier stages it is made up of the closely packed plastic bodies of the creeping myxamoebae, each maintaining, however, its own individual plasma membrane. The myxamoebae, in the process of ripening, transform themselves into fairly thick-walled spores which are oblong bodies about

twice as long as wide. This transformation of the amoebae into resting spores takes place so far as known without any cell division occurring. I have not yet completed the cytological study of *Dictyostelium*, but have so far seen no clear evidence that the amoebae divide at any time during the production of the sorophore or sorus.

The amoebae are surrounded individually and as a mass with more or less slime, and this forms a continuous thin film around the whole sorus when mature. In my observation, however, it never forms a membranous layer comparable to a sporange wall. It is not so abundant that the whole mass could be regarded as a colloidal aggregate, the slime forming the continuum of a two-phase system.

I am inclined to the opinion that the globular form of the sorus is the expression of an active tendency of the amoebae to crowd together as closely as possible. I have emphasized that this globular form seems to be most typical for the species. It is, however, quite common to find that when viewed from the side the sorus is slightly lemon-shaped, with a conical papilla at its vertical pole. This papilla is occupied by the apical end of the sorophore and seems to be the expression of a tendency of the sorus to drag downwards by its own weight on the sorophore which supports it. The base of the sorus in FIGURE 1 also seems to extend downward a trifle around the sorophore. The sorus alone, when regard is not had to showing the sorophore, can be photographed in these hanging drop cultures with the greatest ease and at considerably higher magnifications. FIGURE 4 shows such a view of a sorus suspended in air on the sorophore which is attached far enough below the median plane of the sorus so as not to appear in the figure. The outline of the sorus is perfectly circular, and in view of its highly inhomogeneous makeup is a good example of biological economy of space however its form is achieved.

The base of the sorophore is regularly, as the photographs show, somewhat bulbously enlarged. The sorophore tapers much more rapidly at first than higher up, quite as is the case with the stems of higher plants. The method of support and anchorage in *Dictyostelium* is quite specialized and peculiar to the group. The stipe does not radicate downward. It is embedded in a very considerable mass of slime which adheres to the

substratum and tapers upward enclosing as a sheath the enlarged base of the sorophore. However, owing to the density of the mass, I have not been able to get adequate photographs to show the relations of its parts.

The figures as given illustrate a few of the variations in size and form of the sorocarps as I find them. It is clear that in having an erect, tapering and sometimes branching axis terminating above in a fructification and below in a base specialized for anchorage, *Dictyostelium* has in its form the type of organization which is common to most plants from the fungi and filamentous algae to the higher plants. It lacks only a branching anchorage system to simulate a true cormophyte in its form.

In *Polysphondylium*, with its whorls of rather regularly spaced branches which are progressively shorter toward the apex, the differentiation of nodes and internodes is at least simulated. It is interesting in the light of the methods by which this structure is developed that it suggests so obviously what Child (1915) calls differentiation by axial metabolic gradients, though there is no possibility that the cells at different heights in the sorocarp represent successively different growth stages.

In these stalked forms we have also a typical differentiation into soma and germ plasm, the sorophore being wholly somatic and the sorus wholly reproductive. It is further to be remembered, as noted above, that the Acrasieae include an evolutionary series, beginning with forms in which there is no differentiation of soma and germ plasm, as *Copromyxa*, in which all the cells ultimately become reproductive spores, and culminating in the stalked forms like *Dictyostelium* and *Polysphondylium*, in which the differentiation of soma, the sorophore and germ plasm, the sorus is quite as definite as in the most highly specialized organisms. *Dictyostelium* represents thus a distinct advance in its life cycle and degree of differentiation, beyond such coenobic algae as *Hydrodictyon*, *Gonium*, and *Pediastrum* in which every cell, barring accidents, ultimately becomes reproductive.

CELL GROWTH AND MULTIPLICATION

The stages in the life history of *Dictyostelium* have been fully worked out by Brefeld (1869 and 1884), Van Tieghem (1880) and Olive (1902).

If spores are sown in a drop of dilute dung decoction some of

them may germinate at room temperature within a day or two, and germination may continue for several days. The spore wall is thrown off and the protoplast creeps away as an amoeba. These amoebae divide apparently by constriction. I have not studied the process from the standpoint of its method nor the behavior of the nuclei. Brefeld describes the germination of the spores, and figures very fully the appearance of the amoebae and their division. I have photographed the amoebae at various stages. In FIGURE 7 several of them are shown as they appear when not creeping very actively in any specific direction. Very numerous bacteria are present and appear singly and in clumps among the amoebae. The latter are irregular in outline, indicating pseudopodial activity, but were decidedly sluggish in this particular preparation.

FIGURES 8, 9 and 10 show the myxamoebae in a much more active condition. They are much elongated owing to the pseudopodia being thrust out chiefly in one direction. This is the habitual form of actively creeping myxamoebae, and indicates that they tend to travel in a certain direction for a longer or shorter period, rather than to move aimlessly in this and that direction as shown in Brefeld's figures. The end of the amoeba on which the pseudopods are being thrust out can generally be recognized by its vagueness of outline and appearance of being out of focus. This is of course due to movement during the exposure of the photographic plate. The time of exposure of these figures was from 5 to 15 seconds. This elongated form of the amoebae is characteristic when they come to the aggregation stage and are all creeping more or less directly toward the point at which the sorocarp is being built. At this stage, however, a study of these figures (FIGS. 7–10) shows that, while at certain points the amoebae are lined up as if following each other in a definite direction, in general their long axes show every possible orientation. They are creeping about, feeding and dividing, giving no evidence of any tendency to act in common. I have called attention to the elongated forms of these amoebae but a glance at the figures shows that it is by no means universal, and that many of them show what is commonly described as irregular amoeboid form. Certain of the elongated forms are bent at greater or less angles. The common method of changing direction is not apparently by thrusting out a pseudopod from

the middle, but by changing the direction of the pseudopods at what for the time is the anterior end of the amoeba. I have not determined as yet the number of cell generations through which this independent creeping, feeding and dividing stage persists. Many interesting problems present themselves in this connection as to the relative cyclic behavior of a culture started with one or few spores as compared with those started with many spores, and as to the effect of scant and abundant nutrition and of different kinds of foodstuffs and other chemicals on the length of this vegetative reproductive cycle. As noted above, the experimental aspects of these problems of growth and morphogenesis are left for a further contribution. With the completion of this feeding, growing and dividing stage we have a swarm of independent cells which next proceed to build the sorocarp.

The ontogenetic processes of cell growth and multiplication are thus sharply separated from those of morphogenesis, and there is no posssibility of confusion as to the general interrelations and functions of both types of activity in the production of a symmetrically organized multicellular plant body. Growth and cell division are first completed as independent processes. Cell differentiation and morphogenesis follow as a further series of independent processes.

EARLY AGGREGATION STAGES

As noted above, the sorocarps may be formed at the margin of a hanging drop or scattered irregularly through it. There seems, however, to be a marked tendency in these forms as in the Myxomycetes to seek out the relatively dry regions of the substratum when they come to the fruiting stage. Sorocarps formed on the margin are especially favorably placed for study and for photographing, since the culture substratum, whatever it may be, is especially thin and transparent in that region. The determining factors in the selection of the point at which a sorocarp is to be formed are not easy to make out. The sorocarps are by no means evenly distributed around the margin of the drop. There is no evidence that one-sided illumination or slight variations in temperature affect the matter. Conditions too subtle for our ready discrimination may be determinative.

When, however, a clump of the myxamoebae are found to-

gether, it is at once obvious that, in a considerable radius about them, the remaining myxamoebae orient their movements so as to creep toward the group. Here again the stimuli which determine this specifically oriented movement are not at once obvious. It is not clear whether those which start later are influenced by the existing group or move toward that region because of the same stimuli which guided those which became the first members of the group. In FIGURE 17 an early stage in this grouping is shown and it is at once obvious that the movements of the amoebae are, at least at first, not oriented with any great exactness upon a specific point. The outline of the margin of the culture drop is not at all clear in this figure. It was not an even arc of a circle as in FIGURES 18–21, but was very irregular as in FIGURES 22 and 23. Subsequent observation showed that in this case the sorocarp was built in a projection of the culture drop a little to the left of the center near the top of the figure. A considerable number of amoebae in this region form an oblong group parallel to the outline of the culture drop. The group thins out to the left. To the right its outlines do not come out in the reproduction. Radially inward from this group are two very irregular clumps of myxamoebae. The general orientation of most of them is toward the point where the sorocarp will be formed, but the orientation is not at all mechanically exact.

FIGURES 18 to 21 are from photographs of another sorocarp at successive stages in its formation. They were taken at intervals of fifteen to twenty minutes and show the process of aggregation from a very early stage up to the time when the sorophore is well started and the young sorocarp has pushed up out of the culture medium so that the light from the side strikes it and is reflected upward giving the high light spot near its vertex.

In all these figures as noted the margin of the culture drop is sharply outlined as an arc of a circle cutting across the figure above its middle and the habit of the groups of amoebae to push out onto the glass slide carrying the margin of the culture drop with them is well shown. The effect is to give the group an even drier position in which to start the sorocarp, and is probably an expression of negative hygrotropism at this stage in their development. The sharply rounded outline of the projection is doubtless a matter of surface tension in the liquid culture medium, together with the tendency of the amoebae to crowd together

into as small a space as possible. Such conditions as this show a strong contrast to those shown in FIGURES 7–10 where the amoebae in general are scattered irregularly through the culture drop while feeding, growing and multiplying by division. The change shown is doubtless the expression of cyclic changes in the myxamoebae themselves and may be classed with what are generally regarded as phenomena of maturity. No sexual reproduction has yet been discovered in the group, but the periodic recurrence of this tendency to aggregate is perhaps comparable in a way to the periodic recurrence of the condition which leads to sexual reproduction in forms in which the latter process occurs.

FIGURES 18 to 21 are somewhat less magnified than FIGURE 17, but the elongated form of the amoebae and the orientation of their long axes in the direction toward the forming sorocarp is evident. They are obviously moving both in groups and singly toward a common point where they pack themselves closely together into a rounded cushion-like heap.

As noted, the nature of the stimuli by which the amoebae are guided in forming these aggregations is not obvious. They show some tendency to form radial series as if they were each following a path marked by their predecessors. This arrangement is, however, by no means universal. Many amoebae are scattered as isolated individuals and none-the-less obviously from the orientation of their long axes are seen to be moving quite directly toward the forming colony. This orientation is, however, by no means mechanically perfect. Some individuals are turned a little to the one side, others to the other; an occasional individual is placed quite transversely to the direction toward the group. The positions of the cells show free individual variations but with a very marked tendency to oriented movement in a direction toward the site of the future sorocarp.

IN FIGURE 18, as in FIGURE 17, there are quite irregular clumps of amoebae just back of the centre of aggregation. Outside the region immediately adjacent to the group this figure does not show the amoebae or shows them very faintly. This is, however, a matter of the inadequacy of the photograph. The whole region included by the figure and even further out showed numerous scattered amoebae with more or less definite orientation of their long axes toward the young sorocarp.

IN FIGURE 19, oriented amoebae are shown at much greater

distances from their goal, but here again the photograph leaves much to be desired. The most active amoebae are naturally more blurred than those which are less active. The margin of the group shows a radiating outline, indicating that the myxamoebae maintain their elongated form as they join the mass.

In FIGURE 20 a condition has developed which is of frequent occurrence in connection with the formation of sorocarps on the margin of the culture drop. The amoebae coming in from the left of the group, along the margin of the culture drop, are so numerous that they form a plasmodium-like strand or stream in which they advance by a sort of mass creeping movement toward the young sorocarp. This condition regularly arises in very abundant and well nourished cultures. All of Brefeld's figures show this condition, especially in the region near the forming sorocarp. Further out at the ends of these massed radiating strands he shows the amoebae creeping together more individually to form the strands.

In my cultures these strands are produced as a result of the tendency of the maturing amoebae to creep toward the margin of the drop. This tendency represents an early phase in the fruiting process. They first creep toward the margin of the drop and then converge on the points where the groups are forming. The result is that there are proportionally many more amoebae coming in from the marginal region than from the region radially inward from the group, and these marginal amoebae naturally become aggregated into more or less massive strands. Even if they are not so numerous as to make these confluent masses and still continue to creep individually toward their goal, they are none-the-less likely to be more numerous along the margins. In FIGURE 22, which shows this condition, there is a fine illustration of their interrelations and the general method of their advance to the sorocarp. There is in this case a distinct swarm of them strung out at a slight angle to the, in this case, rather irregular margin of the drop, all headed more or less directly for the group but all behaving quite as independent individuals. There is no more tendency in this case to form a pseudoplasmodium than there is in a swarm of minnows. They show no evidence of following each other directly, though of course it would be hard to prove that each individual might not be following a trail left by some earlier predecessor.

FIGURE 21 represents the last stage photographed in this individual series. The increased blackness of the central group indicates its greater height and opacity. The pronounced high light spot on its vertex indicates that it was well above the surface of the medium so as to reflect the light coming in from the side. There are not many amoebae about it and those that are shown are not so pronouncedly elongated as in earlier stages. The group had doubtless suffered somewhat from the disturbances involved in photographing.

FIGURES 22 and 23 represent stages from the development of other sorocarps selected to show particular conditions. I have referred above to the evidence of individual independence in the movements of the amoebae as shown in FIGURE 22. In FIGURE 23, the development of the sorocarp was checked for some reason at a stage about the same as that shown in FIGURE 21. The difference in appearance of the amoebae in the two figures is obvious. In FIGURE 23, they are angular or rounded and about isodiametric instead of elongated as they are in all the figures in which they are shown in the active creeping condition. In coming to rest the true nature of the pseudoplasmodium becomes obvious. In rounding up, the amoebae draw away from each other, and the fact that they have not fused, as they do in a true plasmodium, becomes conspicuous.

The series as a whole (FIGS. 17–23) illustrates the essential facts as to the method by which the amoebae congregate as free individual cells, each responding for itself and independently to the stimuli which direct this highly specific morphogenetic process. I have referred to the fact that, in Brefeld's and Olive's figures, there is the possibility of interpreting the streaming together of the amoebae as a sort of massed or plasmodial motion, more directly analogous to that in the Myxomycetes. I have studied especially these less crowded cultures, for the sake of making it clear to what degree the coming together of the amoebae in pseudoplasmodia is necessary for, or directly associated with their oriented movement. It seems to me that the distribution and orientation of the amoebae in all the figures (17 to 23) make it clear that the individual cells, as such, are the active and self-determining units in the whole process of coming together to form a sorocarp. In the cultures, the morphogenetic process in these early stages is initiated and carried out by the

cells as such, without any confusing element of mass or aggregate action which might afford opportunity for assuming the existence of some organizing principle, the property of the mass as a whole in accordance with which the morphogenetic process was being carried on. There is no question that the phenomena of true plasmodial movements, and the morphogenetic processes as seen in the Myxomycetes, are regarded as strong evidence in favor of those conceptions of growth and morphogenesis as mass phenomena of protoplasm, rather than activities of individualized cells which Sachs has emphasized.

The formation of the sorocarp in the Acrasieae, by strictly individualized action of the cells, shows most interestingly that there is no occasion for assuming any new method of morphogenetic control in the case of the Myxomycetes beyond what is in evidence in these pseudoplasmodial forms. I have, however, studied crowded cultures like those of Brefeld and Olive, and have prepared even more extreme cases. If the spores are sown abundantly, the amoebae may become so numerous as to form a continuous mass over the glass. FIGURE 16 is a photograph of a small region in such a culture. The amoebae form a nodular and even ridged thick film in which the individuals glide over and around each other but show no connected streaming movement such as is so characteristic of a true plasmodium. The character of the movement affords evidence of the independence of the individual amoebae as Zopf (1885) has illustrated it in his very crude diagram of a pseudoplasmodium. The lower righthand corner of the figure extends into the marginal region of the culture where the depth of the culture medium is less and toward which, as noted above, there is a specially directed movement of the amoebae in the cultures approaching maturity. The effect is in this densely crowded culture to form a thick corrugated or ridged zone which extends around the whole periphery of the culture. The figure shows an arc of this zone extending diagonally across its lower righthand corner. The roughened surface and marginal ridged zone could only be brought out adequately by the use of reflected as well as transmitted light, and hence the magnification used had to be very low.

This culture had reached the fruiting stage and the figure (FIG. 16) shows two young groups of myxamoebae, rather close together. They lie on a diagonal line a little above its center

and appear as two prominences connected by the faint indication of a ridge of amoebae which is more conspicuous near the smaller left-hand group. The creeping movements of the amoebae around and between these two young sorocarps were very active and illustrated a situation not uncommon in crowded cultures but relatively rare in those which are not so densely populated with myxamoebae. The ridge between the two young groups indicates a general tendency of the amoebae to move toward the region of the two groups indiscriminately, without directing their movements specifically toward one or the other. In the immediate region of the ridge the movements were indicative of a conflict of stimuli with a fluctuating variable result. This particular culture was observed for fifteen to twenty minutes, during which it was alternately placed in the damp chamber and on the stage of the microscope for observation, when it became so dry that movement ceased without either *anlage* developing into a mature sorocarp. Movement in the ridge itself was at times toward one and again toward the other of the groups, though such movements never extended entirely to the group away from which the movement was proceeding. The movement on the two sides of the ridge was at times in the same and at other times in opposite directions. The whole picture indicated uncertainty as to whether both or only one of the groups would become a complete sorocarp and was a convincing proof of the delicacy of the stimuli to which the amoebae respond. It is not uncommon to find two completed sorocarps as close together as the two young groups in this figure, but in such cases as a rule one sorocarp is much smaller than the other and was evidently formed later by amoebae which came together after the larger sorocarp was completed or well advanced in its development. The two extremes of monospore cultures on the one hand, and these sown with great masses of spores on the other, need careful comparative study under controlled conditions and with variation of environmental conditions.

FORMATION OF THE SOROPHORE AND SORUS

The stages immediately following that shown in FIGURE 21 are particularly difficult to obtain under conditions making it possible to photograph them. The mature forms, as shown above, can be photographed in hanging drop cultures with low mag-

nification, but I have found no way of photographing the intermediate stages *in situ* with sufficiently high magnification to bring out the desired details. I have had to resort to the method of pushing such stages over and covering them as they lie in the culture medium with a cover glass. This of course results in great disturbance of the masses of myxamoebae in their relation to the sorophore and the slime masses which they secrete and in which they are more or less imbedded. However, the observations of Brefeld (1884), Olive (1902), Zopf (1885) and Van Tieghem (1880) agree as to the essential facts for these stages and the photographs I have obtained confirm the figures and descriptions of these authors. Olive's figures are especially clear and diagrammatical.

The myxamoebae which form the initial group, compact themselves into a rounded mass, the sorophore initial, imbedded in slime. The anchorage of the mass and the maintenance of its orientation to the substratum are effected by the slime which the amoebae have secreted. When once this base of the future sorocarp is established the amoebae proceed to pile themselves upon its vertex and build it higher and higher. The primary orienting stimulus in erect cultures, it seems to me, is that of maximal resistance to motion, without, of course, loss of contact with their fellows. The amoebae glide in that direction in which the greatest resistance is offered to their motion. We may call this the stimulus of maximal resistance and its obvious relation to the principle of functional hypertrophy is at once suggested. As shown in inverted cultures, negative hygrotropism is also involved. This reaction brings them, even in the earliest stages, to the exact apex of the rounded mass produced by their primary movements of aggregation. Those myxamoebae which succeed in reaching a certain area of maximum downward pull have reached apparently a position of equilibrium and proceed very gradually at first to build rigid walls and pass into a condition something like encystment.

Up the stalk so formed the mass of amoebae, as they arrive, continues to climb, and at its vertex they contribute themselves to its further elongation upward. The amoebae at these stages are regularly numerous enough to form a pseudoplasmodium and the entire young sorophore is enclosed within it. As it becomes still higher its apex remains enclosed in an oblong pseudoplas-

modial mass. Below this, however, the pseudoplasmodium narrows to a rounded strand applied to one side of, or spirally coiled around, the sorophore but not enveloping it on all sides. I have obtained a figure of this stage (FIG. 11) which shows a segment of the sorophore made of the compacted amoeboid cells to the right and the pseudoplasmodial strand attached to it on the left. The pseudoplasmodial mass shows faintly the outline of the individual amoebae, though as the preparation was much disturbed and some minutes intervened in its preparation for photographing, it would not be safe to assume that these appearances are normal or represent the shape of the myxamoebae as it is in the actively creeping mass.

A comparison of the cells making up the sorophore at this immature stage with those in the ripened sorophores shown in the figures in PLATE 8, shows that at this stage they are more rounded, less flattened upon each other, and give less the appearance of a typical parenchyma. It is evident that the achievement of their definitive forms by the cells of the sorophore is a slow process. In this figure the thin sheath of dense slime which envelopes the sorophore can be recognized as a continuous structure, especially at the points where it bridges the gaps between those cells which are so rounded in outline as not to fit closely together.

This zone of uncompacted cells which still retain their capacity for amoeboid changes in form is apparently relatively longer in the later stages of sorophore formation. The fact that in the figures (FIGS. 11 and 12) the cells are rounded rather than amoeboid in outline, together with the bends and irregularities in outline of the sorophore in the same figures, is quite possibly due to disturbance during the preparation for photographing. FIGURE 12 shows the same young sorocarp in a region a little higher up where the pseudoplasmodial strand is just widening out into the oblong apical mass. The sorophore occupies the median vertical axis of this mass and at once supports it and the pseudoplasmodial strand as it continues to glide upward. This figure is much less magnified than FIGURE 11.

FIGURE 13 shows a short segment of this apical pseudoplasmodial mass with the young sorophore in its centre. The magnification in this case is approximately the same as in FIGURE 11. In this figure the cells are still more rounded and less compacted than in FIGURE 11, and the thin slime sheath of the soro-

phore is well shown. It is obvious that as the sorophore reaches greater height the whole structure becomes more and more unsteady, and the possibility of maintaining a position of maximum resistance to downward pull becomes more and more difficult. The myxamoebae, by bending of the whole sorocarp or by shifting of the pseudoplasmodial mass, are brought into new relations to the downward pull and prevented from keeping the equilibrium point. They are thus compelled to carry on for longer and longer periods those delicate readjustments of form and position which give the gentle upward curves of the sorophore and maintain the balance of the pseudoplasmodial mass. These readjustments may be characterized as functional morphallaxies and constitute the most delicate of the morphogenetic responses by which the symmetrical and adaptive form of the sorocarp is achieved.

FIGURE 14 shows the apex of a young sorocarp at about this stage of development. The more or less rounded outlines of the individual amoebae are quite definitely shown over the apical surface and further back, though here again it would not be safe to assume that the living cells have not changed their form as the result of the manipulation. This figure shows clearly the trumpet-shaped widening of the sorophore sheath at its upper extremity. This form of the sheath has been observed by Brefeld (1884), and Olive (1902). In such stages it would seem that the sheath as first secreted by the amoebae may be much wider than its later diameter and that it narrows gradually as the cells within take on more and more their permanent form and space relations in the ripe sorophore. A cytological study of stained sections of this as well as other structures and stages in the formation of the sorocarp may be expected to bring out further structural details which may make more clear both the nature and the origin of the sheath.

We are particularly in need of light on the nature of the creeping process by which the pseudoplasmodium raises itself upon the stalk which it simultaneously is building at its upper end. The behavior as to form changes, etc., of the myxamoebae in a pseudoplasmodium, as compared with the pseudopodial motions they show when creeping as free individuals, needs much further study. That we are still far from agreement as to the cell structures and their relations and functions in ordinary pseu-

dopod formation in the larger amoebae is clear from Mast's (1923) recent new analysis of the whole process and his very interesting conclusions as to the relations of the various surface layers of the cell to each other and to the formation of pseudopods in the process of creeping.

As the height becomes still greater the possibility of maintaining a position in the centre of downward pull reaches a limit and the myxamoebae give up the effort and "consent to be elected to the germ plasm." This critical point, when the capacities of the myxamoebae for functional morphallaxis are overtaxed may, of course, be reached at various points according to the total size of the pseudoplasmodial mass: when the upper cells of the sorophore are still approximately isodiametric; when they are horizontally flattened discs; or when they have become vertically elongated in a ratio sometimes as high as 1 to 4 or more. In a given environment this will be a matter of the relation of the diameter of the sorus to the cross-section of the sorophore. We find thus a natural self-limiting factor, an organic regulation without entelechie, which determines the height of the sorocarp. An adaptive result is thus achieved in an entirely indirect and incidental fashion. The capacity to respond to the stimulus of maximal resistance has no direct and necessarily natural connection with spore dispersal as such.

The final stages in the formation of the sorocarp consist in the cessation of sorophore formation under the conditions just described and the completion of the ascent of the pseudoplasmodial mass upon it. The rounded pseudoplasmodial strand shown in FIGURE 11 withdraws upward until it forms a part of the oblong apical mass. This mass gradually contracts upward until it forms a more or less perfect globe on top of the sorophore as shown in FIGURES 2 to 5, or the slightly lemon-formed type with apical papilla shown in FIGURE 1. These variations are due perhaps to differences in the degree of favorableness for the completion of the ripening processes.

The number of spores contained in a sorus can be determined rather readily by bending over a sorocarp just before maturity till the sorus touches the glass substratum. The spores then spread out in a film with the sorophore in the midst and can be readily counted. FIGURE 15 shows a photograph of such a preparation. The spores extend out in a projection at the upper

left following an extension of the film of moisture in which they lie. The number of spores in this case is approximately 1300. The possibility of readily determining in this way the spore number produced in any given sorus and culture is of significance in connection with the problems of life cycle as affected by the initial spore number sown which were referred to above.

We can distinguish roughly three regions of the sorophore which differ in the rate at which it tapers. This is more or less obvious in FIGURE 1, though the outlines of the sorophore are too vague to permit accurate measurements in this case. First, there is a short basal region in which the diameter diminishes very rapidly. This is the more or less bulbous base. Second, there is a median region in which the reduction of diameter goes on much more slowly and in which there may be regions which are almost perfectly cylindrical. This portion corresponds to that of a tree trunk above the radiating base and extending in forest grown trees to the branches or further. Third, we have the terminal region in which the sorophore tapers more rapidly and in which we may even find its individual cells vertically elongated. I have determined the ratio of length to width in a series of photographs of parts of sorophores and in PLATE 8 have reproduced a number of figures illustrating the degree of tapering in form at various heights and from sorocarps of various sizes.

FIGURE 24 shows a segment from near the base of a rather large sorophore and is a massive parenchymatous aggregate. It is impossible to get more than a surface view of the outlines of the cells in a photograph, since the tissue is too dense to show anything in a median optical plane. However, enough is shown to indicate that the cells in general take the theoretically to be expected surface tension form and show in optical section from five to seven or eight sides. In the center they might be expected from the method of their aggregation and getting their shape by mutual pressure to appear as the tetrakaidekahedrons which least surface conditions would require (Lewis, 1923).

In a region where the sorophore has from four to six cells in cross-section (FIG. 25) as would be expected the cells are still approximately isodiametric. The taper in this figure is approximately at the rate of 1 to 112; that is, there is a reduction of 1 unit in diameter to every 112 units in length. This is a slow rate of decrease, and that it is maintained with comparative constancy

through considerable series of cells shows how delicate the responses must be by which it is achieved. There can be no recourse in such a case as this to the assumption that this gradual tapering is the expression of surface tension in the whole sorophore. It is achieved, just as it is probable the tapering form of plant stems and trunks generally is achieved, by the specific response of the living cells to factors of their external and internal environment. It is at once obvious that there can be no principle of organization operating in the whole swarm of myxamoebae to determine the form of the sorophore as a whole.

The sorocarp is not formed as an evolutionary unfolding of a growing mass but by the spontaneous assembling of free independent and mature cell units, whose capacity for delicately adjusted response to stimuli gives the mature structure its symmetrical and highly adaptive characters. As noted, morphogenesis is here shown as an independent process in no way dependent on growth or cell division, further than that these processes furnished the cells which carry out the morphogenetic processes.

The number of cells in the cross-section of the sorophore diminishes gradually with its tapering form. In FIGURE 26 we have a segment in which the number is reduced to two or three in its basal end and diminishes still further to two and then one at its upper end. The cells at this level in the sorophore tend to become wedge-shaped and flattened horizontally instead of remaining isodiametric as in the thicker portions of the stipe further down. The result in median optical section of the sorophore is to give somewhat the appearance of saw teeth interlocking with each other. The cell walls form a rather conspicuous more or less regular zig-zag line down the middle of the sorophore.

At the upper end of the segment shown in FIGURE 26 there is a rather sudden narrowing of the sorophore in diameter and a corresponding reduction in the number of cells in cross-section from two or three to one. The taper from the basal region to the region just below this more sudden narrowing is at the rate of about 1 to 103. If we include the whole length of the segment the rate of narrowing is about 1 to 48. The transition from a cross-section of two or three cells to one is perhaps a critical point and may involve more rapid change in the rate of tapering.

Not all sorophores show such an even rate of tapering as is indicated by such cases as those shown in FIGURES 25 and 26. In FIGURE 27 we have a segment of about the same general character as that shown in FIGURES 25 and 26, but it shows no such regular tapering form. Its fluctuations in diameter as visible at once to the eye are not great, but they are of an order of magnitude comparable to those which constitute the normal tapering itself. Basing the estimate on measurement of the diameters at the two ends of the segment, the taper would be 1 to 533, but in such a case these measurements can have little significance. Another segment of about the same character as to the number of cells in its cross-section and which is not so irregular as the one first considered, is shown in FIGURE 28. This segment of sorophore shows almost no measurable taper and illustrates the tendency in the median region of the sorophore to show a very slight or no progressive reduction in diameter for considerable distances.

FIGURES 25 to 28 are all from different sorocarps, and illustrate the variation in tapering and shape of the cells which characterize the middle region of the sorophore. The remainder of the figures belong to the upper or terminal region. We can consider them best in two groups. FIGURES 29, 30 and 31 are characteristic of wild growing large sized sorocarps. FIGURES 32 to 36 are from the less well nourished and much smaller sorocarps grown in hanging drop cultures such as were used for the study of the behavior of the individual amoebae in the growth and aggregation stages as described earlier. The two groups are quite different in the shape of their cells. In the second group the cells are much elongated vertically, while in the first they show no such elongation and are regularly disk-shaped, their transverse or horizontal axes being longer than their vertical axes.

In FIGURE 29 we have a segment of the terminal portion of a sorophore in which the number of cells in cross-section fluctuates from one to three. Those cells which fill the entire cross-section have transverse diameters two to three or more times their vertical diameters. In the cases where two cells fill the cross-section they tend to be wedge-shaped. The taper in this section is 1 to 67, much more rapid than that in the middle region of the sorophores as shown in FIGURES 25 to 28.

In FIGURE 30 is shown a portion of a sorophore made up of

disk-shaped cells of almost uniform size, with their width, the diameter of the sorophore, uniformly greater than their height. Near the middle of the segment a cell is broken and the transverse walls of the adjacent cells are curved out toward it, showing that turgor is still present in these cells even in the mature sorophore. This sorophore segment shows no easily measurable taper, a condition much less common in the apical than in the median region.

The part of the sorophore included in the sorus is sometimes less even in outline than that below. This condition is illustrated in the terminal segment shown in FIGURE 31. In this case the apex of the sorophore is turned to one side. Back of this it swells slightly and then narrows again. Lower down a cell is broken or missing as in FIGURE 30 and there is the corresponding outward curvature of the walls of the adjacent cells. The segment is made up of a single series of cells as in FIGURE 30, but they are less uniform in shape and size. The transverse septa are quite diagonally placed in a number of cases. There is nothing on the sorophore to mark the point at which it passes out of the sorus in these figures. The slime which coats more or less all the parts of the sorocarp has no definite significance as a peridium such as we find about the spore mass in a myxomycete.

The remainder of the FIGURES 32–36 are as noted from much more slender and smaller sorocarps. In FIGURE 32 we have a segment made up of disk-shaped cells which are quite irregular in size and with cross diameters much exceeding their height except near the upper end of the segment. The tapering is quite uniformly at the rate of 1 to 55. This is the most rapid rate of diminution in diameter shown in any of the portions of sorophores figured.

In the section of sorophore shown in FIGURE 33 the cells again are quite irregular in size and here, as in the upper part of FIGURE 32, we find many of them higher than they are wide. This is characteristic of the terminal region of the slender sorocarps grown in drops of dilute dung decoction, and comes to even more extreme expression in the sorophores shown in FIGURES 34 and 35. Somewhat above the middle of this segment a cell was broken in mounting the preparation. The segment (FIG. 33) tapers at the rate of 1 to 70.

It is obvious in FIGURE 33 as in the previous figures that the

relative vertical space occupied when any two adjacent cells are compared is not alone a matter of their relative position in the sorophore, but also of their actual relative size as produced in the growing and multiplying period. This is shown conspicuously in these terminal segments of the sorophores by the casual way in which the longer and shorter cells are distributed.

The important morphogenetic fact to be noted in these terminal segments is, however, the further striking change in cell form which in these cases the terminal position brings with it. We can note now the culmination of the series of changes in cell form which are involved in the production of the evenly tapering sorophore. At the base we find cells which are approximately isodiametric and take more or less typical least surface forms by mutual pressure. This condition continues in the lower median region. In the upper median region and the lower part of the terminal region we find the cells somewhat flattened, as the number of cells in cross-section is reduced to two or three. This flattening is still more conspicuous higher up in the terminal region. The condition so far might suggest a direct flattening effect on the cells with increased height. But when we come to the upper part of the terminal region we find the relative length of the horizontal and vertical axes of the cells gradually reversing itself and the cells becoming elongated upward.

This condition is very clearly shown in the segment of a sorophore shown in FIGURE 34. I have measured the transverse diameters and heights of the cells beginning with the first cell completely shown at the basal end as number 1. The relation of width to height varies from 1 in width to 6 in height, to 1 in width to 4.6 in height in this series. The average for this single segment of a sorophore is 1 in width to 2.1 in height. I have also measured the widths and heights of the cells in the section of sorophore shown in FIGURE 30, which, as noted, is from a larger sorocarp grown on its natural substratum. This type of sorocarp is illustrated in FIGURE 15. The magnification is very low in this case but an examination of the sorophore just below the sorus shows that the relative widths and heights of its disk-like cells are of the same general order of magnitude as those shown in FIGURE 30. The range in the proportions of these cells is from 1 in width to .3 in height to 1 in width to .7 in height. The average here is about 1 in width to .4 in height. We see that in

the terminal region of the small sorocarp the cells may average over twice as high as they are wide while in the terminal region of the larger sorocarp they may average less than half as high as they are wide. The relations of width to height in all the cells of these two figures are given in TABLE I.

TABLE I *Showing relation of cell width to cell height in segments of two sorophores from their terminal regions. The cells are numbered from the base of the segment upward beginning with the first cell which is fully shown in the figure.* FIGURE 30 *from a large sorocarp taken from its natural substratum.* FIGURE 34 *from a smaller sorocarp grown in a hanging drop of horse dung decoction.*

	FROM FIGURE 30		FROM FIGURE 34	
Cell	*Width*	*Height*	*Width*	*Height*
1	1	.6	1	1.4
2	1	.5	1	.8
3	1	.7	1	1.2
4	1	.3	1	.6
5	1	.6	1	1.1
6	1	.3	1	1.1
7	1	.4	1	1.9
8	1	.4	1	1.0
9	1	.5	1	2.4
10	1	.4	1	1.7
11	1	.4	1	1.8
12	1	.6	1	2.2
13	1	.5	1	3.3
14	1	.4	1	2.9
15	1	.5	1	4.1
16	1	.6	1	4.5
17	1	.4	1	4.6
18	1	.5	..	.....
—	—	—	—	—
Av.	1	.47	1	2.1

The number of cells measured is not large enough to give an adequate statistical picture of the general situation, but the tendency is unmistakably in the direction indicated. An extended statistical study of these variations would be well worth while, and I am collecting material for it.

The fact that the morphogenetic response of the cells can be reversed so strikingly from the base to the apex of the same sorophore, in the extreme case from proportions of 1 in width to 1 in height, as is common in the basal region of all sorophores, to 1 in width to 4.6 in height (cell 17, FIG. 34) is the point with which we are particularly concerned. We have here the proof that cells, all of the same colony, presumably of about equal age, and probably belonging approximately to the same cell generation from the spore, can show such great and highly adaptive variations in form, depending on the position in which they happen to find themselves in the sorophore. Such morphogenetic responses as this are plainly in the same general category of cell reactions as those which lead to the differences in cell proportions which we find between bast cells and parenchyma, for example, or as any of the other responses affecting cell proportions which we find in the histogenetic development of the higher plants.

FIGURE 35 is from a very poor photograph of the same sorophore shown in FIGURE 34. The rate of tapering in FIGURE 34 is 1 to 61, and in FIGURE 35 it is 1 to 65. The two figures overlap in part. The second entire cell shown at the base of FIGURE 35 is the same as cell 13 counting from the base in FIGURE 34. The relation of width to length becomes even more extreme in the uppermost cells, going as high as 1 in width to 6 in height. The apex itself does not come out in the reproduction, though shown in the negative. The end cell is slightly widened and there is more or less waste material about it such as is also shown about the apex of the sorophore in FIGURE 31.

The section of sorophore in FIGURE 36 is given to show that the protoplasts still have considerable mass in all these young sorophores, though it is not recognizable in the photographs. In this figure the protoplasts are shrunken and their shrivelled masses are conspicuously shown. The cross walls are sometimes obscured by the material deposited on them. The preparation suggests that in fully formed sorophores the cells may be still alive. The rate of tapering shown in FIGURE 36 is 1 to 78.

MORPHALLACTIC CURVATURE

I have discussed the morphogenesis of the sorophore from the standpoint of the simplest case, that of a straight, vertically erect tapering column. As a matter of fact, the sorophores are

never absolutely straight but curve variously, all the while maintaining their generally well balanced posture. The most conspicuous case of controlled curve production is that which appears when the sorocarp develops on a sloping or inverted substratum. The sorophore is built out vertically to the substratum for a certain distance in response to negative hygrotropism and then curves upward as a result of negative geotropic response. Such a curvature is not as it is in practically all other cases a so-called growth curvature. The curvature is accomplished by increasing the number of cells on the convex side of the curve or by morphallactic rearrangement of the material of the cells so that they are more or less wedge-shaped with the thinner edge toward the concave side. In such gentle curvatures of the sorophore as are shown in FIGURE 26, it is not at all easy to determine which method or whether both methods have been involved. Such curves are undoubtedly produced at the upper end of the sorophore while the cells are not yet compacted. As noted before, this rounded uncompacted condition of the cells extends (see FIGS. 11 and 13) some distance below the apex of the sorophore and doubtless indicates the limits of the zone in which such curvature adjustments are possible. The evidence for delicacy of response in this case is as noted very striking.

Such regulatory responses for maintaining erectness must be in evidence throughout the development of the sorocarp, since in nature pressure of air currents, as well as slight shifts in the position of the load supported as the decidedly topheavy pseudoplasmodial mass creeps upward, must be continually occurring and require continual slight compensatory shifts in the protoplasmic masses of the cells in the uncompacted zone. Mechanically it would appear that these responses must be, in the case of upright cultures, in the nature of upward thrusts against any increase of the load on a particular flank of the sorophore. The case is similar in this respect to that of functional hypertrophy in growing organs. Here, however, as stated, the sorophore does not increase in height by growth, and the process involves either the shifting of entire cells near the apex, or change in form of the cells, implying a shift of their protoplasmic material. Olive reports also an increase in volume of the cells as they become vacuolated. In either case it is a matter of morphallactic readjustment of mass and the response as in the case of tapering

may be designated as functional morphallaxy to indicate its parallelism with functional hypertrophy. Here again, from the standpoint of morphogenetic theory, the conspicuous fact is that free and individualized cells are able by morphallaxis to duplicate so perfectly the curves and symmetry adjustments which we regard so generally as strictly growth phenomena.

BRANCHING SOROCARPS

It has been observed by Brefeld (1884), Olive (1915) and others that *Dictyostelium* occasionally branches. Such a case is shown in FIGURE 5. As Olive has well described, the process consists in simply developing a lateral sorocarp on the main sorophore as a base. The two then form parts of a single symmetrically balanced whole. As the photograph shows, the sorophore of the branch was accidentally broken and bent back upon itself at about three-fourths of its height. The sorus of the branch rests back upon its sorophore in the figure.

The branching of *Dictyostelium* is very simple as compared with the development of the rather evenly spaced verticils of branches of successively diminishing length found in *Polysphondylium*. Olive's studies show that morphogenetically the process is the same in both cases. The branches are duplicates of the main axis in all their structures and are attached to it in the same fashion as it is attached to the general substratum. As noted above, it is not easy to bring out the structure of the base of sorocarps so as to show the basal bulb and its enveloping slime separately because of the density of the mass. The same is true for the origin of branches. Olive's drawings are very clear, and my observations confirm his entirely. In FIGURE 6 is shown with higher magnification the region of origin of the branch of the plant. At this level both the main axis and the branch are shown to be made up respectively of single series of disk-like flattened cells. The branch starts from the main axis at an angle of about 33°, but soon curves in and runs more parallel with it. The branch originates on the upper surface of the curved main axis in a position well adapted for its support. Aside from the accidental position of the sorus of the branch the whole makes a well balanced figure. The sori before the breaking of the branch were rather close together, the sorus of the branch lying somewhat below the plane of the figure. The upper surface

of the base of the branch can be traced almost to the surface of the main axis. Its lower surface is much more obscured by the enveloping slime which forms a broad clasping base partly enveloping the main axis. The curved upper surface of the slime as it fills the axil of the branch gives full expression to the play of forces to which it is subjected in anchoring the branch to the main axis. The basal end of the branch is rounded off and is not moulded in any way to the surface of the main axis. Its attachment to the latter is entirely a matter of the viscosity and distribution of the slime mass. The slime is, of course, entirely inert and its distribution about the base of the branch is due to the rounded form of the mass of amoebae which congregated at the point of origin of the branch. The whole effect is to produce a highly movable and elastic joint. Such a well balanced branching figure illustrates the possibility of producing by morphallactic cell aggregation the same plant habit whose outlines as noted above we associate with and are wont to assume can only be produced as growth curvatures.

THE REGULATION OF TAPERING

The work to be done in the morphogenetic processes involved in forming the sorocarp is primarily the lifting of a certain load. That this is not a constant load throughout the process is clear, but, as noted, a number of factors are involved in its variation, whose relative significance is not at once obvious. It might be assumed that at first, while the pseudoplasmodial mass rests largely upon the substratum, the load would be at its minimum. On the other hand, the upward thrust at this stage is against the surface tension of the mound of slime and myxamoebae formed by the aggregation processes. Just how great this is as compared with the weight resistance later is not clear. For a certain period the pseudoplasmodial mass is increased by the addition of further amoebae which creep in from the neighborhood as the figures show. As soon as the sorocarpic mass rises above the surface of the culture medium, there can be no question that a drying-out process begins and is accelerated through all the subsequent stages. It may well be that this progressive drying-out is the most important of all the factors influencing the weight of the mass. Brefeld (1869) emphasized the significance of the slime envelope which covers the whole mass, and speaks of a

point in the development of the stalk when this slime membrane is broken away from the slime remaining at the base of the stalk.

There is no doubt that the weight of the load carried by the developing sorophore at any particular stage is determined by a complex of factors whose adequate analysis will be difficult. It seems to me, however, that at least when once the pseudoplasmodial mass is lifted from the substratum, it will undergo progressive loss in weight by drying and further, comparing the weight of the pseudo-plasmodial mass as a whole at the initiation of sorocarp formation with the weight of the full formed sorus, there can be no doubt that a more or less progressive loss in weight has occurred. We must not forget that those myxamoebae which mould themselves into the tissues of the sorophore as it is formed, thereby remove their own weight from the load to be carried by those above them. Taking all the factors in the situation into account it seems to me it is safe to assume a progressive loss of weight in the load to be carried, especially after the very early stages, and that this diminishing load may be reckoned with as a morphogenetic stimulus.

Perhaps the most notable structural feature of the sorophore as described above and shown in the figures of PLATE 8 is its smoothly and evenly tapering form. We naturally associate this characteristic with an assumption of progressively diminished load to be carried. We have noted that in the erect cultures the production of a vertical column of some sort is provided for by the capacity of the cells to react to stimuli of maximal resistance. This morphogenetic response is basic for the production of the sorophore. The tapering form and gentle curves of the finished product demand further analysis. Taking the whole situation into account it seems to me the factor of relative load carried at different heights is the one to be first considered.

Accepting the conclusions reached above, as to the general result of all the factors affecting the weight of the pseudoplasmodial mass, we may call this the stimulus of diminishing load. This stimulus again, we may assume, operates to induce functional morphallaxies which may effect readjustments in the space relations of entire cells or in the form and distribution of mass of the individual cells. We can not, however, think of such a stimulus as producing a constant alteration in the form of the cells, as, for example, that successive diminution in load

will always produce corresponding increase in the length of the vertical as compared with the transverse axis of a cell. The facts as described above contradict such an assumption. The responses, by which the stimulus of diminishing load controls the tapering form of the sorophore, vary with the height and the general size of the whole sorophore mass. Marked increase of the height as compared with the width of the cells only occurs under certain special conditions described above. The taper in the larger sorophores involves a reduction in the number of cells in the cross-section. That this change can be brought about, not by controlling the rate and plane of cell division, but by the form-determining responses of a group of cells, is the striking morphogenetic fact to be noted. Further, in the analysis of the whole question as to how the general proportions of the sorocarp are determined and the degree of tapering in the sorophore is regulated, we are confronted, as in the case of the coenobic algae, with a sort of symmetry response. There is, it seems to me, evidence that cells will manifest morphallactic readjustment in order to come into symmetrically distributed contact and pressure or tension relations, as far as possible, on all their surfaces. The capacity to respond to the stimuli of maximal resistance and diminishing load, and the functional morphallaxies which give expression to the results of these stimuli, suggest the sensitiveness of the cells to all forms of pressure and contact interrelations. The stimuli of maximal resistance and diminishing load are probably supplemented by these more delicate relations of mutual contact and pressure in the transverse axis of the sorophore. Contact responses may be dependent on stimuli resulting from varying degrees of adhesion between the cells as they dry and ripen out in the maturing of the sorocarp. However brought about, these symmetry responses are very strikingly characteristic of *Dictyostelium*, as well as of morphogenetic phenomena in the higher plants.

DISCUSSION

Pressure and contact stimuli. If we consider further the question as to the nature of the stimuli concerned in determining the morphogenetic responses of these colonies of myxamoebae, it seems to me that, as in the case of the coenobic algae, we are forced to regard as of great importance these cellular interre-

lations of contact and pressure. The behavior of the myxamoebae in hanging drops shows that neither gravitational nor moisture stimuli are entirely dominant. And it seems probable that the general orientation of the sorocarps to the substratum is determined by the joint effect of negative hygrotropism and negative geotropism. These are the stimuli which direct the creeping upward or downward of the pseudoplasmodium, just as they influence the direction of growth of plants in which growth and morphogenesis go on simultaneously. When we consider the tapering form of the sorophore, its bulbous base and the progressive changes in the relation of height to width in its cells, the stimulus of diminishing load seems to be of primary significance. Curvatures are probably of two general types, those determined by the general hygrotropic and geotropic reactions of the pseudoplasmodium, and those which maintain the general balanced posture of the sorocarp. Both involve morphallactic adjustments in the distribution of entire cells and in the form of individual cells and are achieved in the apical undifferentiated region of the sorophore. The upward movement against gravity is a response to the stimulus of maximal resistance. In downward growth negative hygrotropism would operate similarly through a stimulus of maximal dryness. The parallel in many of these cases with growth responses is striking, but it is to be remembered that here the responses are all achieved by discrete individual cells and that there is no possibility of interpreting them as mass reactions of protoplasm. Primarily such pressure and tension relations are all matters of weight stimuli, the expression of gravitation acting in the field of intercellular relations. The condition of intercellular contacts, partial or complete, may also develop stimuli in connection with the adjustment of the cells to each other as they gradually compact themselves in the sorophore.

The grounds for such assumptions are, it seems to me, fairly clear. The sorophore is primarily a supporting structure. Its proportions of height to width are obviously adapted to the load it has to carry. The building of the sorophore provides for lifting the germ plasm into an advantageous position for drying out and distribution as dustlike spores. The formation of the sorophore involves two morphogenetic elements, the secretion by the amoebae of the inert slime envelope and the aggregation and

deposit successively upon each other of the amoeboid cells. In the simplest cases in which the sorophore consists of only one series of cells, this involves simply the placing of one cell upon another, at first as rounded bodies and later by compacting as disks or shorter or longer tapering cylinders. The outstanding morphogenetic fact is the exactness with which the cells adjust their forms and intercellular contacts so as to produce the evenly tapering outline of the sorophore as a whole. Just how far the secretion of the slime sheath is related to this form regulation is not clear, nor is it entirely clear whether the sheath is a product of the surrounding cells or those in the sorophore itself. In any case the inert slime belongs in the category of cell wall materials and it is a well established fact that it is the protoplast rather than the wall which determines the form of a cell. In the slime sheath, then, or in producing the slime sheath, each cell adjusts itself to those proportions in length and width, which will give just such a reduction in the diameter of the sorophore as will maintain its even taper. When we consider how slight these dimensional changes are, the delicacy of the response is seen to be almost inconceivable.

Furthermore, the cells must make such an adjustment of the distribution of their masses as will develop the curves which the common reaction of all the cells to the environmental stimuli of moisture and gravity require. Doubtless the slime sheath which is secreted serves in some degree to maintain the smoothness of outline of the sorophore, but the morphallactic response by which curves arise must be a matter of direct cell response.

Brefeld (1869, *pl. 3, fig. 21*) figures a case which shows the sheath developed as an empty tube beyond the contained amoeboid cells. I have never seen such a case, and it is not easy to see how it could have arisen, as the whole upper end of the developing sorocarp is a continuous mass of myxamoebae. Brefeld introduced the confusing conception of free cell formation here and his description is not clear. In his first paper, Brefeld (1869) was of the opinion that the amoebae during sorocarp formation fuse to form a true plasmodium, a view which he later corrected (1884). That the sheath once formed aids in support of the sorophore is clear, but as an inert slime its thickness, diameter, etc., must be determined by the cells which secrete it. As noted above, at least in the later stages, it is trumpet-shaped at its

upper end (see FIG. 14) and this condition may persist in less degree in the ripe sorus. That the tapering of the sorophore is not perfectly uniform nor progressively modified from base to apex in any simply mechanical fashion is clear from the figures I have given. None-the-less, in these respects it is quite like axial structures in plants generally. A basal region of rapid tapering is followed by a median region of slight or no tapering and the apical region again tends to taper more rapidly.

In general symmetry of proportions and adaptations for securing spore distribution the sorocarp of *Dictyostelium* compares favorably with *Mucor* or other molds in which the growth and morphogenetic processes are combined as they are in the higher plants.

Relation to older theories of ontogeny. As to the bearing which the facts of morphogenesis in *Dictyostelium* have on the older theories of ontogenetic development, it seems to me certain rather definite suggestions are obvious. It is clear that no preformational, mosaic or promorphological representation of the mature sorocarp in the spore is possible. The position of the cells in the sorocarp, their differentiation in form and their ultimate fate as soma or germ plasm are all matters which are determined after the long period of growth and cell division in the free swarming colony is completed. It appears that those amoebae which are earliest to mature or are most vigorous and active in initiating the morphogenetic processes will come to form the sorophore. The remainder of the amoebae will form the sorus and constitute the germ plasm.

For studying the evolutionary differentiation of soma and germ plasm we have, as noted, in the Acrasieae a fairly complete series. There can be no question that this differentiation has been achieved progressively as an adaptive modification, all of whose stages can be assumed to have selection value. As the process works out in ontogeny we are confronted with a striking example of the disregard of the interest of the individuals, here the cells, as compared with those of the species. The very cells which initiate and carry out the process of building the sorophore are sacrificed in the interests of giving the remainder "a better place in the sun." I have pointed out in another connection that the tendency of cells to achieve balanced and symmetrical relations of mutual contact and pressure may be a basic feature

in our appreciation of the aesthetic value of symmetry and balanced proportions. In view of the very obvious suggestion of self determination in many of the cell activities in *Dictyostelium*, it is possible to interpret this action of the myxamoebae in building the stalk on which their fellows may climb to a more advantageous position as a very primitive form of altruistic expression.

That there can be no fixed predisposition of any of the amoebae for any specific part of the sorocarp is well shown by Olive's experiments in which he placed partly developed sorocarps in fresh culture solutions and observed the myxamoebae separate and then renew their morphogenetic activities, by building not one but several new sorocarps, instead of reconstructing the one upon which they were engaged when interrupted by the experiment. These facts of morphogenetic behavior in *Dictyostelium* are to be considered together with the long established fact that certain sponges, when cut up into fragments, creep together and reunite to form new sponges, and the familiar facts of the development of totipotent blastomeres as strong evidence against all mosaic theories of development.

Greil's revival of epigenetic conceptions consists in hardly more than a renewed recognition of the conception that inheriting is achieving. The emphasis thus placed on all forms of morphogenetic stimuli, internal as well as from the external environment, is quite in accord with the evidence for the importance of cellular interactions as shown by *Dictyostelium*. The difficulties in the application of simple epigenetic conceptions to the analysis of the development of the sorocarps in *Dictyostelium* are, however, just as obvious as in the case of more complex forms. In assuming that the cell organization of the myxamoebae and the cormophyte-like organization of the sorocarp are fundamentally dissimilar, I am not assuming any lack of complex organization in the myxamoebae. The specificity of the spores in these simple types is quite as definite as is that of the germ cells in the higher plants. The nature of this specificity is suggested by the character of the reactions by which the sorocarp is built and by the cyclic changes in the reactions of the amoebae at successive stages in their cellular development. What I have called the maturity which marks the end of cell growth and cell division, and is followed by sorocarp formation, may be the result of a cyclic metabolic change such as Child (1915) emphasizes.

His assumption, however, that morphogenetic processes must necessarily be the expression of such changes in growth processes, is not in accord with the facts of sorocarp development. The structure of *Dictyostelium*, and even more that of *Polysphondylium*, with its successive whorls of progressively shortened branches, seems to illustrate very perfectly Child's conception of serially developed structures which owe their differentiation to axial gradients in metabolism. The facts clearly show in this case, however, that just such metameric symmetry in form, with corresponding histogenetic differentiation and variation in prospective function, can all be produced by morphogenetic processes carried out by a colony of cells which grew and divided under similar environmental conditions, and presumptively belong to the same, or almost the same, cell generation. I shall leave the further evidence as to the general organization of the myxamoeba and the relation of the facts of sorocarp formation to Child's theories, to be discussed further in connection with the experimental study of morphogenesis in *Dictyostelium*.

Organic regulations. The morphogenetic processes involved in the formation of the sorocarp, as noted earlier, may bring with themselves regulatory stimuli to limit the height of the sorophore. Increase in height of the sorophore carrying the mass of myxamoebae will bring increasing unsteadiness calling for more continuous morphallactic readjustments in the cells of the axial region. When this increase reaches a certain point it may serve practically to prevent the cells from forming the normally compacted type of tissue in the sorophore. This condition may result in inhibitory stimuli which prevent further cells from moving into the apical region of the sorophore.

Another variable which may afford organic regulation in respect to height is found in the relation of weight carried to the cross section of the sorophore. A remote approach, even, to the crushing point for its cells may serve to prevent the addition of further cells to the sorophore. Whether or not the height of the sorophore is regulated by these particular factors in the situation, the possibility of the internal production of organic regulations in such a process is strongly suggested. Given a system of plastic cell units capable of responding to stimuli which lead to morphallactic readjustments in the distribution of their inter- and intra-cellular mass relations, whose function it is to raise a

shifting and unsteady load to a height well within the crushing limits of the system, the intercellular pressure relations may be conceived as providing the stimuli which will determine the height to be reached.

Organization of the cell of the metaphyte. Lundegårdh (1914) in one of the more recent attempts at a statement of a so-called chemo-physical theory of life phenomena, makes as a basic working hypothesis the assumption that there is in principle no difference between a unicellular and a multicellular organism since the latter is merely "a heap of cells," all of which have the same makeup, and this makeup is chemo-physical. This hypothesis should be capable of clear illustration in the case of *Dictyostelium*, since the sorocarp is visibly in its origin "a heap of cells." But the evidence that the organization of the sorocarp is the same as the organization of one of the myxamoebae that built it is certainly not obvious. Such a statement puts an extreme emphasis on the conception of the individual, whether one- or many-celled, which it seems to me is opposed to all the fundamental facts which have come to constitute the cell theory. Lundegårdh everywhere emphasizes the conception of the cell as a mechanism, but in claiming the equivalence of one and many-celled organisms he does not sufficiently recognize the fact that, in simple phrase, machines are not aggregates of smaller machines of the same kind.

I have elsewhere stated the grounds for regarding protophytes and metaphytes as incommensurables from the standpoint of their organization; and the facts as to the structure and life histories of such forms as *Dictyostelium* and *Polysphondylium* are, it seems to me, further evidence for the correctness of this assumption. To compare the erect radial and metameric plan of organization of *Polysphondylium* with the amoeboid form and protoplasmic constitution of one of the cells which helped to build it, is to overlook, as Lundegårdh does, the essential and obvious facts of observation in the interests of a generalization so broad as to have lost all important concrete content.

The specificity of many-celled organisms is in general most obvious at least in their form characters, and it is the *morphogenetic* predispositions and capacities of the cells that are most in need of analysis. In *Dictyostelium* it is to be noted that all of the morphogenetic cell capacities which we have postulated

involve the functioning of the cell body as a whole. The morphogenetic processes by which the sorocarp is organized out of the discrete myxamoebae are matters of cell responses in which the cell behaves as a unit organism. The sorocarp is an organized aggregate of myxamoebae, but the myxamoeba is a biologic unit and not an aggregate of organisms.

I am aware that my analysis of the complex processes of form differentiation in *Dictyostelium* is incomplete and on many points inadequate, but that these transition types between protophytes and metaphytes present the same problems of morphogenesis, though in a simpler form than that in which they are presented in the higher plants, it seems to me can hardly be questioned.

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Explanation of plates

All the figures are of *Dictyostelium mucoroides* Bref., and the photographs were made with the Zeiss apochromatic objectives 8 mm. and 16 mm., and compensating eye pieces, except FIGURES 1 to 5 and 16, which were made with the Zeiss microplanars.

Plate 6

FIG. 1. Entire sorocarp in hanging drop culture photographed from above, showing that the sorophore, after being built downward for a short distance under the influence of negative hygrotropism, curves into a horizontal direction as a response to the joint stimuli of negative hygrotropism and negative geotropism. × about 20.

FIG. 2. Two entire sorocarps with curving sorophores grown and photographed as in the case of FIG. 1. × about 10.

FIG. 3. Sorocarp with very short sorophore grown and photographed as in the case of FIG. 1. × about 10.

FIG. 4. Sorus photographed as in the case of FIG. 1 to show globular form. × about 60.

FIG. 5. Branching sorocarp photographed as in the case of FIG. 1. × about 10.

FIG. 6. More highly magnified view of region of connection between branch and main axis. × about 50.

FIG. 7. Slowly moving myxamoebae in stage of growth and multiplication with many bacteria in culture medium. × about 300.

FIGS. 8, 9, 10. Actively creeping myxamoebae from three different cultures. × about 300.

FIG. 11. Portion of sorophore with pseudoplasmodial strand ascending on it.

FIG. 12. Portion of same sorophore higher up, where the pseudoplasmodial strand expands into the apical mass.

FIG. 13. Portion of terminal pseudoplasmodial mass showing the sorophore in its median region.

FIG. 14. Apex of pseudoplasmodial mass showing trumpet shaped form of the upper end of the sorophore.

FIG. 15. Portion of sorophore and sorus with spores spread out in thin film.

FIG. 16. Portion of culture with myxamoebae forming a continuous nodular film. The lower right hand corner of the figure extends into the marginal region of the culture, where the amoebae had accumulated to form a still thicker corrugated zone which extended around the entire culture. In a diagonal line a little above the middle of the figure are shown two rudiments of sorocarps between which the myxamoebae are creeping back and forth.

Plate 7

FIG. 17. Very young aggregation stage. The young sorocarp, is forming in a very faintly shown projection of the margin of the culture drop in the upper part of the picture. × about 300.

FIGS. 18, 19, 20 and 21. Show successive early stages in the formation of the same sorocarp. The margin of the culture drop in each case is shown as a clean cut more or less perfect arc of a circle extending across the figures well above their

middle regions. The myxamoebae push out the margin of the culture medium, apparently as a negative hygrotropic reaction. They are shown creeping towards the sorocarpic aggregations singly and in rudimentary pseudoplasmodial strands. × about 250.

FIG. 22. Shows a young sorocarpic aggregation with single myxamoebae creeping toward it, primarily from the marginal region to the left. × about 250.

FIG. 23. Shows a young sorocarp whose development has been checked. Most of the myxamoebae in or near the sorocarpic aggregation have separated slightly from each other and are more or less rounded up. × about 250.

Plate 8

FIG. 24. Portion of sorophore from base of a large sorocarp. Cells forming parenchymatous tissue. × about 1000.

FIG. 25. Portion of sorophore from median region. Taper 1 to 112. × about 1000.

FIG. 26. Portion of sorophore from median region showing a rather abrupt narrowing near its upper end. Taper from base to the region of abrupt narrowing 1 to 103. Taper for whole length 1 to 48. × about 1000.

FIG. 27. Portion of sorophore from median region showing rather uneven outlines. × about 1000.

FIG. 28. Portion of sorophore from median region. No measurable taper. × about 400.

FIG. 29. Portion of sorophore from terminal region. Taper 1 to 67. × about 1000.

FIG. 30. Portion of sorophore from terminal region. No measurable taper, but the middle region slightly narrowed, perhaps because of the loss of a cell. × about 1000.

FIG. 31. Portion of sorophore showing its apex as it ends in the sorus. Outlines rather uneven. × about 1000.

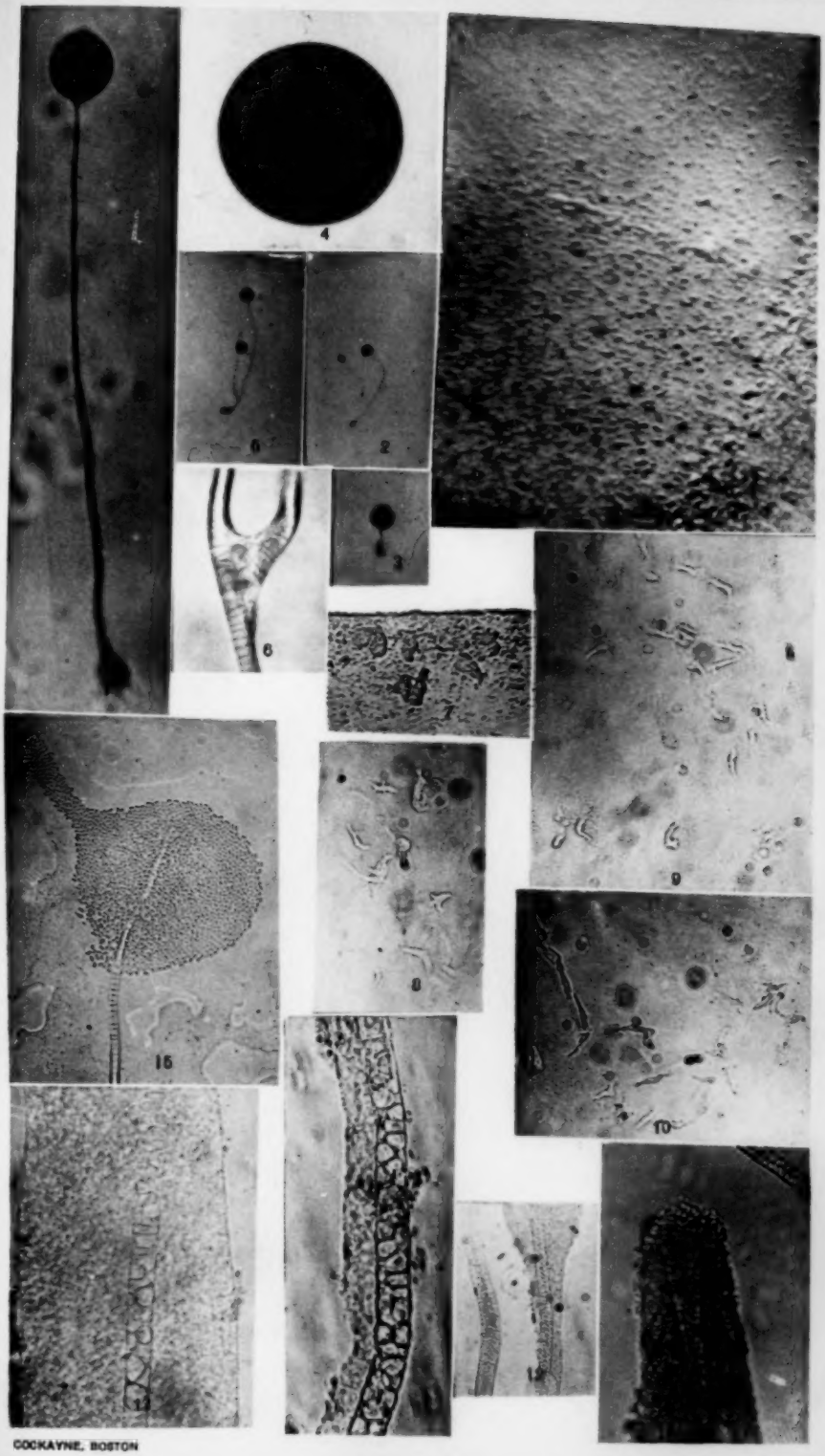
FIG. 32. Portion of sorophore from terminal region. Taper 1 to 55. × about 500.

FIG. 33. Portion of sorophore from terminal region. Taper 1 to 70. × about 500.

FIG. 34. Portion of sorophore from terminal region. Many cells elongated upward. Taper 1 to 61. × about 500.

FIG. 35. Apical region of same sorophore as shown in FIG. 34. × about 500.

FIG. 36. Portion of sorophore from terminal region. Protoplasts collapsed and shrivelled. Taper 1 to 78. × about 500.



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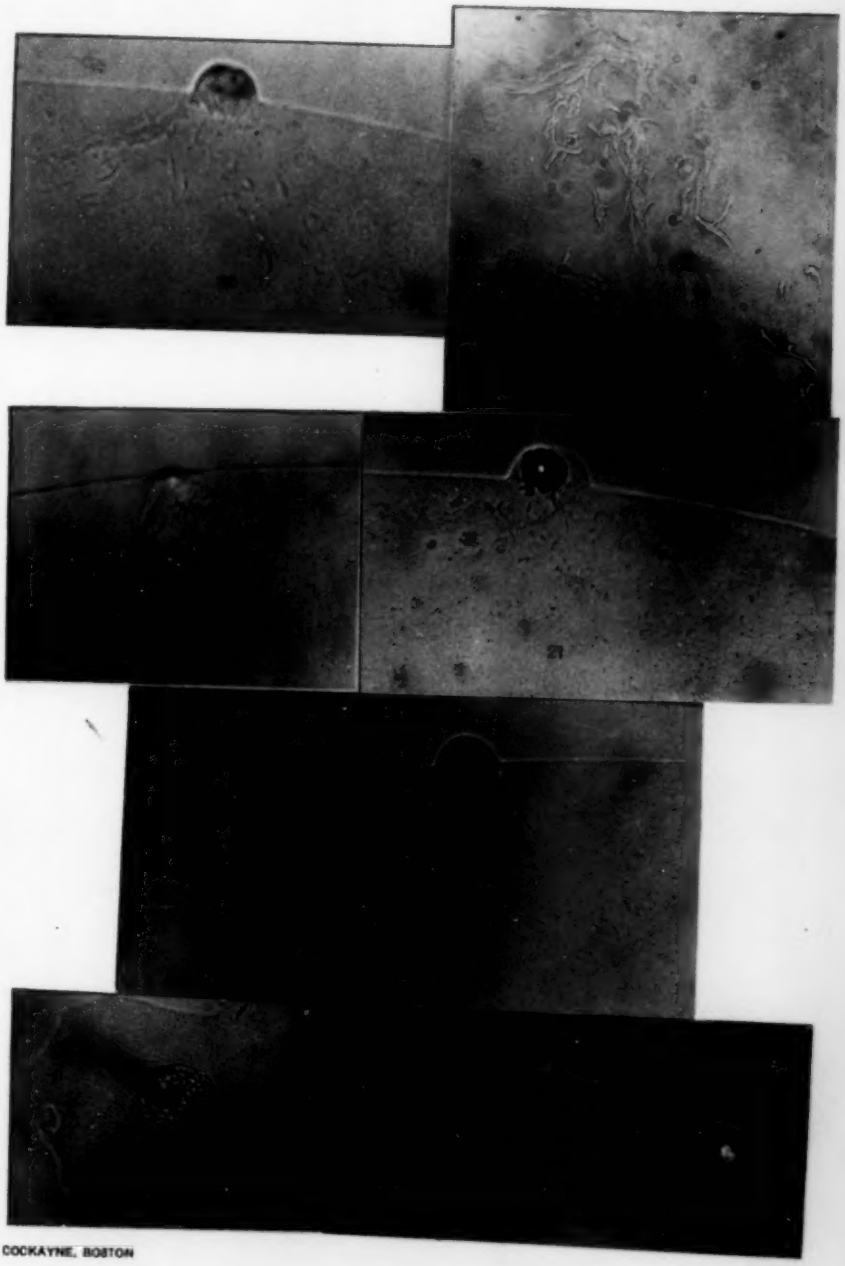

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UNIV OF MICH

The capsules, seed, and seedlings of the tiger lily, Lilium tigrinum

A. B. Stout

(WITH FOUR TEXT FIGURES)

For at least fifty years, tiger lilies have been rather widely cultivated in European and American gardens. The bulbs of this lily first came into England as early as 1804, and there have been many shipments of the bulbs of tiger lilies to Europe and America from the Orient, and especially during the last fifty years of trade relations. At least five varieties differing in some particular from the general type of the tiger lily have come into culture.

As far as the writer has been able to determine, there is no record that any of the tiger lilies have ever been self-fruitful. There is oft repeated mention that they have been entirely fruitless. There seems to be no record, at least outside of Japanese or Chinese literature, as to how these varieties originated—whether from seeds or as bud sports. Apparently the propagation of all the types of tiger lilies has been entirely vegetative by means of the divisions of the mother bulbs and the use of the bulblets which are abundantly produced as buds along the stems in the axils of the leaves.

In the Orient the tiger lily has been in cultivation, it is said, for more than a thousand years. There it evidently exists in cultivation and as an escape far beyond its original habitat. Mr. Ernest H. Wilson, who speaks from much personal observation in the Orient, states of this lily in his recent book "The Lilies of Eastern Asia,"

> In China I have seen it undoubtedly wild on the foothills of the Lushan range in Kiangsi province, but nowhere else. In western Hupeh and in Szech'uan I often met with it apparently wild, but close investigation always proved that it has escaped. I believe that it is indigenous on the mountains of Chekiang and Kiangsu provinces in eastern China, and regard the Lushan range as marking the western limit of its distribution.

But Mr. Wilson has never seen capsules on this lily in the Orient. In a letter to the writer dated January 29, 1926, he makes the following statement:—"During my travels in the Far East I never saw *Lilium tigrinum* bearing fruit." Evi-

dently no person has seen such capsules, for all persons who have discussed the lilies of the Orient, and some of these have travelled rather extensively in those lands, repeatedly state that the capsules of the tiger lily were to them unknown.

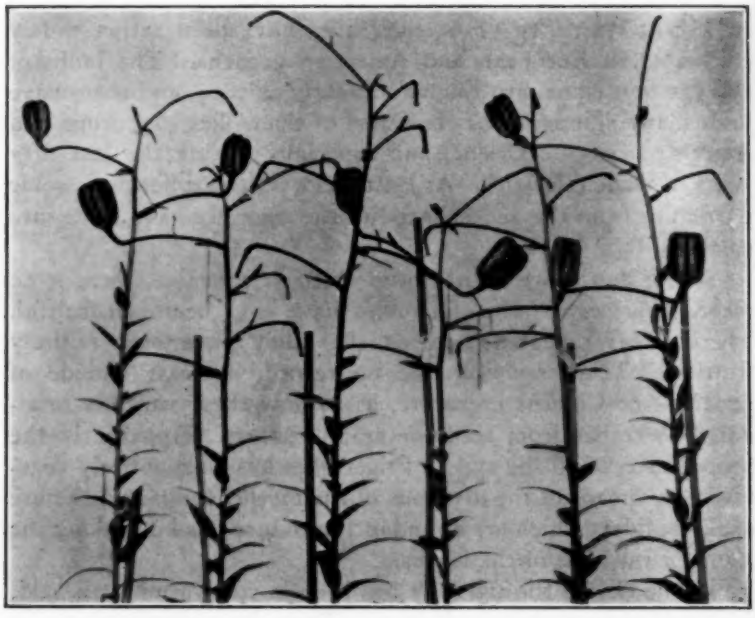

FIG. 1. When there is proper cross-pollination with certain other types of lilies, tiger lilies will produce such capsules as are shown above. This opportunity almost never occurs as the plants are grown in gardens. When the flowers are self-pollinated, or when pollination is from flower to flower on different tiger lilies, capsules do not even start to develop. But sister flowers properly cross-pollinated yield large capsules. The tiger lilies have not lost the ability to bear fruit and seeds because of vegetative propagation. The capsules here shown are from pollen of *L. sutchuenense*, and were obtained in 1923 at the New York Botanical Garden.

THE TIGER LILY IS HIGHLY FRUITFUL IN CROSSES WITH CERTAIN OTHER KINDS OF LILIES

Except for the plants of the *flore-pleno* type, which have aborted pistils, all plants of tiger lilies are highly fruitful in crosses with certain rather closely related species. At the New

York Botanical Garden plants of the tiger lily have yielded capsules and viable seeds to the pollen of four different kinds (species?) of lilies.

To the pollen of *Lilium Maximowiczii*, and *Lilium sutchuenense* about 100 fine capsules were obtained which yielded several

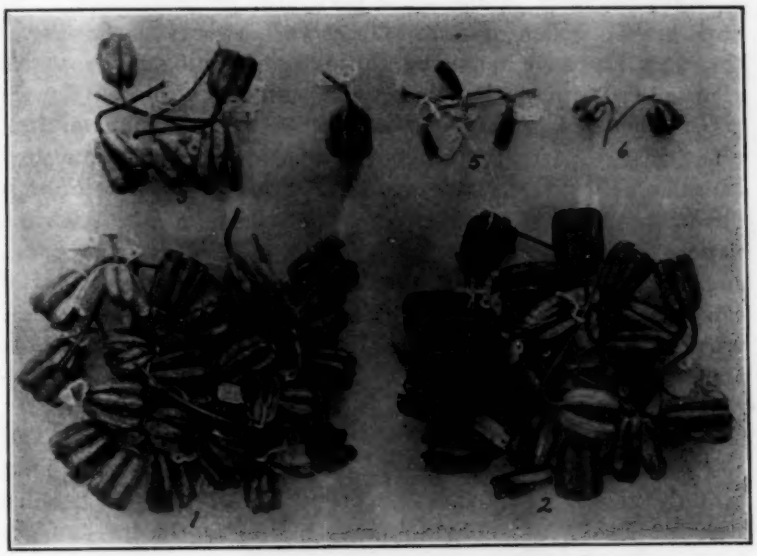

FIG. 2. At *1* above are shown capsules of the tiger lilies obtained from pollination with *L. sutchuenense*, and those at *2* are from pollen of *L. Maximowiczii*. Those two crosses give such capsules as these for nearly every flower pollinated. At *3* are shown some of the capsules obtained from the cross *L. tigrinum* × *L. Leichtlinii*; at *4*, one of the capsules resulting from the use of pollen of *L. dauricum Wallacei*. Thus far in the experiments at the New York Botanical Garden tiger lilies have yielded only such immature and seedless capsules as are shown at *5* to pollen of *L. warleyense*. At *6* are shown capsules obtained on *L. warleyense* when the pollen of a tiger lily was used in controlled pollination.

thousand viable seeds. Some of these capsules were shown (Stout, 1922, 1923) in what appear to be the first illustrations ever published of an authentic capsule of the tiger lily. The two species just mentioned closely resemble the tiger lily in general appearance, and the ease with which they cross with it suggests a close kinship.

These results clearly demonstrate that the flowers of the tiger lily are fully able to function in producing fruit. The plants have not lost their ability to yield fruit and viable seeds. They merely require a proper cross-pollination with certain other types. When this is done, anyone may obtain seeds and grow the hybrid seedlings.

Capsules with viable seeds may also be secured in other crosses. To pollen of *Lilium Leichtlinii*, twenty-six flowers of the tiger lily gave ten good capsules containing many viable seeds and sixteen partly developed capsules. Of thirteen flowers given pollen of *L. davuricum Wallacei* two were complete failures, nine yielded partially developed capsules, and two matured capsules with a few viable seeds. The species *L. Leichtlinii* is obviously rather closely related to the tiger lily. Although the variety *Wallacei* is listed as a variety of *L. davuricum* or *L. elegans* it has a flower of rather striking resemblance to that of the tiger lily. The tiger lilies do not set fruit so readily in these crosses as they do with *L. Maximowiczii* and *L. sutchuenense*. One experiences a greater number of failures. The requirements for fertilization are more exacting and less compatible.

The seeds obtained in all these crosses have been planted and the seedlings which survive will be grown to maturity. Thus far only one has bloomed. It has the *L. sutchuenense* as a pollen parent. This plant does not have bulbils in the axils of the leaves. Its flowers somewhat resemble those of the tiger but differ slightly in color and in spotting (see FIG. 4).

To pollen of several other species, the tiger lilies have given mostly complete failures and only occasionally a poorly matured capsule. Thus far only such results have been obtained when pollen of *L. warleyense*, *L. pseudotigrinum*, and *L. Batemanniae* was used. Of all the lilies thus far studied by the writer those of *L. Leichtlinii* and *L. pseudotigrinum* most closely resemble *L. tigrinum*, yet of these two only the former has successfully crossed with it.

The true identity of the plants obtained under these species names is a matter on which the writer does not wish to attempt a final opinion. Mr. Wilson in "The Lilies of Eastern Asia" does not recognize some of them as good species. The plants which the writer obtained under these different names were clearly of somewhat different and distinct types. If not good species they were at least varieties.

In the pollinations thus far made at the New York Botanical Garden, capsules have not even started to form on tiger lilies to cross-pollination with the species *auratum*, *canadense*, *candidum*, *chalcedonicum*, many varieties of *davuricum*, *Henryi*, *Humboldtii*, *Roezlii*, *speciosum*, *superbum* and *umbellatum*.

OTHER RECORDS OF CAPSULES PRODUCED BY PLANTS OF LILIUM TIGRINUM

The cross *L. tigrinum* × *L. Maximowiczii* has also been successfully made by Miss Isabel Preston (1924, 1925 and 1926).

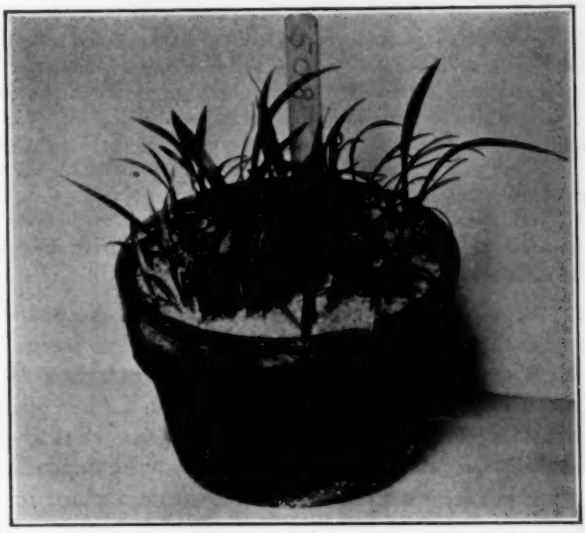

FIG. 3. Lusty seedlings may be had from the hybrid seeds obtained on tiger lilies. Those here shown have *L. Leichtlinii* as the pollen parent.

Her first seed to this cross was secured in 1921 but this was not reported in print or known to the writer until after his publications of 1922. Miss Preston illustrates a flower of this hybrid, which is evidently similar to the one here shown in FIG. 4.

Miss Preston also reports having obtained seeds to the cross *L. tigrinum* × *L. warleyense* (*L. Willmottiae*) and she shows a photograph of the hybrid in flower. This cross has repeatedly failed at the New York Botanical Garden.

Mention is made by Miss Preston of seedlings of *Lilium speciosum* × *L. tigrinum* produced at the Ontario Agricultural College, which, however, never grew to flowering size.

In a report of certain hybridizations made about twenty years ago in Australia (Kerslake, 1906) there is the mere statement that the cross "*L. tigrinum* × *L. elegans Wallacei* resulted in every flower operated upon producing huge pods of seed." This cross is one of those which has succeeded at the New York Botanical Garden.

In his beautifully illustrated monograph on the genus *Lilium*, Elwes (1880) makes the following statement in reference to *Lilium tigrinum:*—

> Everywhere in China and Japan it is cultivated and the bulbs are eaten by the natives: but I never saw the capsules and seeds though they are figured by Nees von Esenbeck, 'Genera Plantarum,' vol. II. Mr. Hanson, of New York, informs me that he has been successful in raising many seedlings from this plant, some of which differed remarkably from the parent, both in the form and color of the leaves and flowers: but, owing to a fire which destroyed the whole of these seedlings, I am unable to describe them more particularly.
>
> Mr. Hanson says that to induce the plant to seed, all the bulblets must be removed, and that the seeds, if sown at once in a frame, germinate quickly and produce flowering plants in three or four years.

It may be said that the capsules figured by Nees von Esenbeck and labelled as those of "*Lilii tigrini*" are included in a plate with flowers, flower parts, and a bulb of *Lilium Martagon* to illustrate the various parts of a typical lily. The capsules are longer and of a somewhat different shape than those the writer here illustrates. It is perhaps doubtful that the capsules drawn for the plate in Genera Plantarum came from a plant of *Lilium tigrinum*.

The statements of Elwes, quoted above, make it clear that Mr. Hanson obtained seed from plants of the tiger lily and grew the seedlings. But Mr. Hanson is in error in considering that the removal of bulblets axillary to the leaves led to the production of the seed he obtained. Evidently he was merely reflecting a rather popular view which has survived even to the present time. Mr. Hanson had, it is stated by Elwes, "one of the finest collections of lilies in the world." Without a doubt he grew plants of *Lilium tigrinum* by the side of such species as *L. Maximowiczii* and the insects made the cross-pollinations which were responsible for the capsules which he obtained from his

tiger lilies. That he obtained fruit when he removed bulbils was merely a coincidence. Had he enclosed the flowers of such plants in paper bags and prevented all pollinations except selfings his plants would have been fruitless.

It is really surprising that results such as Mr. Hanson reported have not been observed rather frequently. While the species named above which readily cross with the tiger lily are rarely

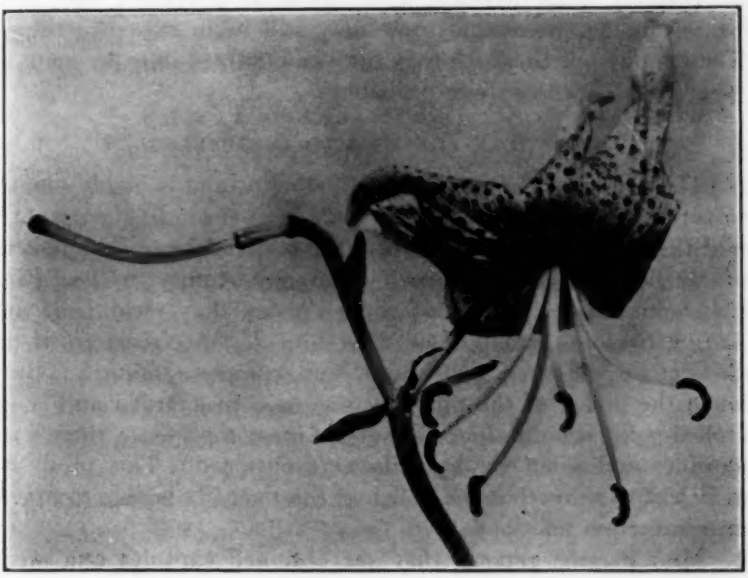

FIG. 4. Flower of a hybrid lily having the tiger lily as its seed parent and *L. sutchuenense* as its pollen parent. The plant does not bear bulblets oh the stem and the color of the flower and the spotting are slightly different from the seed parent.

seen in gardens, it is to be expected that they may be grown along with *Lilium tigrinum* in the gardens of fanciers of lilies and in nurseries concerned with producing lily bulbs for the trade. Especially may this be expected to occur in the Orient.

Evidently at least one such hybrid has appeared. In an English garden magazine *The Florist* for 1873, the flower of a lily was illustrated in color, and described as *Lilium tigrinum* variety *Lishmanni*. It differed from the tiger lilies in having no

bulbils, in the smaller size of the flowers and in somewhat different color and spotting. Evidently this plant was very similar to that which the writer shows in FIG. 4 accompanying this article.

One type of lily cultivated by the Chinese in Yunnan has been considered as a hybrid between *L. tigrinum* and *L. tenuifolium*. But Mr. Wilson in his recent book already mentioned assigns this plant to the species *L. Davidii*.

Possibly other hybrids, seedlings of *L. tigrinum*, have appeared in the Orient and some may still be in existence there. The readiness with which they may be obtained in experimental breeding makes this quite probable.

THE TIGER LILY AS A POLLEN PARENT

The pollen of the tiger lilies is abundant and is highly viable in artificial culture. A high percentage of the grains germinate and there is a vigorous growth of the pollen tubes. The pollen is excellent. There has been little opportunity to use this pollen in the reciprocals of those crosses that yield fruit on *Lilium tigrinum*. Only four flowers of *L. Maximowiczii* were thus cross-pollinated and these were complete failures. But when the pollen of the tiger lily was used in guarded and controlled pollination on four flowers of *Lilium warleyense*, three fine capsules and some viable seeds were obtained. This result is sufficient to show that the pollen of the tiger lily is able to function in certain relations.

Miss Preston reports that she obtained capsules and seed from flowers of *L. speciosum* pollinated from the tiger lily but that the seeds did not germinate. This cross has always failed at the New York Botanical Garden.

The writer has thus far found no other references to the experimental use of *L. tigrinum* as a pollen parent in breeding work.

THE TIGER LILIES ARE ENTIRELY FRUITLESS TO ALL POLLINATION AMONG THEMSELVES

During the past ten years more than 200 bulbs of the tiger lilies have been secured from various sources for use in experimental studies at the New York Botanical Garden. These include bulbs of the type most usually seen in cultivation, of the varieties *Fortunei*, *splendens*, and *flore-pleno*, and also of plants

apparently wild at Kuling, obtained by Dean J. L. Buck, of the University of Nanking, China. About half of these various lilies have lived to bloom. Many pollinations were made, both of individual flowers and from flower to flower on different plants. In no case did a capsule even start to develop. In the first years of study the bulblets were not allowed to develop in the axils of leaves for a number of the plants. In these tests the entire race of tiger lilies has been entirely self- and intra-sterile. This behavior is quite in agreement with the many reports that the tiger lilies have been fruitless. The results of the experimental studies confirm the observations of the gardeners.

IS THE TIGER LILY A GOOD SPECIES OR MERELY A CLONAL VARIETY?

Since the tiger lilies do not produce seeds to any sort of pollination among themselves there is no seed that can be used to propagate their kind. They yield seeds only to cross-pollination with different types of lilies and this gives hybrids different from the tiger parent. The evidence indicates that the tiger lilies have always been propagated exclusively from daughter bulbs and the stem bulblets. If this be the case, then the tiger lilies do not constitute a good species breeding true from seed, but merely a clonal strain or variety.

Such a variety has its beginning as a single seedling which is ever afterward propagated vegetatively. In the case of the tiger lily this seedling may have been a hybrid or it may have been a variant from some other type of lily now extinct or perhaps considered as a distinct species.

There is, however, a possibility that the tiger lilies do not constitute a single clonal group and that further search may discover different clonal strains that are cross-compatible. A collection of tiger lilies from widely separated localities in Japan and China would allow one to make more satisfactory tests for this than have thus far been possible. It is even possible that there are localities in China where tiger lilies are really wild and propagating by seed.

THE TYPE OF STERILITY IN THE TIGER LILIES

The flowers of the tiger lilies, excepting only the double flowered form with its aborted pistils, are perfect. The pistils are able to develop into capsules. The pollen is highly viable

and will function in certain relations. The plants are fully able to mature at the same time both fruits with viable seeds and bulbs and bulblets. They are self-fruitless because the essential organs—the pistils with their ovules and eggs and the pollen tubes and their sperms—do not react in the manner necessary for fertilization. There is, one may say, a physiological incompatibility in the processes of fertilization necessary for seed formation.

This type of sterility is indeed very common among plants, both wild and cultivated, that have perfect flowers. It exists among annuals that are propagated only by seeds. It is present in plants that are propagated vegetatively and in this case the plants of the same clon will not "cross," for the pollination between plants is not crossing but is in reality only the same as pollinating from flower to flower on one plant.

Sterility from self-incompatibility is the rule in all of the thirty odd species of lilies tested at the New York Botanical Garden. Even in species that commonly yield seed abundantly (*L. regale*, *L. longiflorum*, *L. Henryi*, *L. speciosum*, *L. superbum*, *L. tenuifolium*, etc.) many seedling plants are as completely self-incompatible as is the tiger lily. But in these the species includes numerous clonal strains and is grown from seed rather generally. Although there is also some cross-incompatibility between plants known to be different seedlings, there are usually, in a planting of these lilies, enough different strains to provide for compatible crossings. Abundant capsules and seed on the lilies in one's garden almost always mean that there are different seedlings or clons present and that the insects have made cross-pollinations between them.

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Abnormalities in Botrychium and certain other ferns

M. A. Chrysler

(WITH FIVE TEXT FIGURES AND PLATE 9)

Abnormalities in the spore-producing members in *Botrychium* have been frequently reported, and many unusual specimens are to be found in the larger herbaria, yet a comprehensive analysis of the variations has apparently not been made. Taxonomic writers have for the most part contented themselves with a mere mention of the occurrence of abnormal spikes (Pretz, *14*) or with a list of the forms encountered in a specific area (Batchelder, *2*). Luerssen (*12*) however, has grouped the "monstrosities" of *Botrychium Lunaria* in twenty-two classes, and his three main groups will be followed here. In the present paper it is proposed to offer some analysis of the writer's observations of the genus *Botrychium* in field and herbarium, and to show the bearing of aberrant forms in other ferns upon the interpretation which is offered.

The following classes of abnormalities may be distinguished:

1. Branching or duplication of the fertile spike, as a result of: (*a*) Splitting or chorisis. (*b*) Wide separation of an ordinary branch. (*c*) Reversion.
2. Occurrence of sporangia on pinnae ordinarily sterile.
3. More or less complete sterilization of the fertile spike.

1. With respect to forked or otherwise divided fertile spikes, the writer (*8*) has already committed himself to the view that specimens of *B. obliquum* Muhl, *et al.*, having a pair of spikes in place of the single one, represent a reappearance of an ancestral condition, and from this view he sees no reason to recede, but it does not appear that certain of the forked specimens found in other divisions of the genus can be thus interpreted. The doubt in these cases arose from the fact that in forking specimens of *B. virginianum* (L.) Sw. the two branches are generally unequal. In May 1924, an opportunity was afforded for examining the vascular supply of a forking specimen, for two of these interesting plants were found by the writer near New Brunswick, New Jersey. Each of these examples was a vigorous plant two feet high, and had a fertile spike which forked rather unequally at a point half way up the stalk. The forking region of one plant

was cut into serial sections, and the vascular strands traced. It has been shown (*8*) that the vascular system of a normal spike consists of a right and a left hand strand, derived respectively from points near the right and left edges of the C-shaped vascular strand of the petiole. In our forking spike there was the usual pair of strands below the level of the fork, each strand being more or less broken up, as is frequently the case in this species. Where the spike forked a portion of the left-hand strand accompanied the right-hand strand into the right fork, leaving somewhat less than the left-hand half to supply the left fork of the fertile spike, which fork was the more slender of the two, as might be expected. This procedure is in marked contrast to the state of affairs in specimens of *B. obliquum* possessing a double spike, for in these the right-hand strand supplies one spike and the left-hand strand the other spike. This difference in the vascular supply in forking specimens belonging to two different divisions of the genus led the writer to suspect that there are at least two independent phenomena which should be distinguished. With this idea in mind he has recently examined all of the specimens of *Botrychium* which were readily available, and has found an unexpectedly large number of cases of branching spikes, amounting to over 170, located in the Academy of Natural Sciences of Philadelphia, Brooklyn Botanic Garden, New York Botanical Garden, University of Pennsylvania, Yale University, United States National Museum, and in several smaller collections. As the study proceeded it became evident that practically all of the branched spikes in *B. virginianum* were divided unequally, generally very definitely so. The location of the fork may be at almost any level, from near the base of the fertile spike to near the spore-bearing portion. The abnormality may occur in large specimens and also in depauperate individuals, and is represented by plants from a wide range (New England, Japan, Ecuador for instance). Dr. Kelley has called my attention to a large forking specimen in his collection which had been damaged by a falling branch. Although most specimens show no evidence of wounding, such stimulus would probably have to be exerted in the preceding year upon the embryonic leaf, and hence would not show in the mature leaf except in the form of such abnormality as has been described. It is at any rate submitted that such stimulus as a wound may bring about a splitting of the apical

region of a young leaf, a phenomenon referred to by Bower (*4*) as chorisis, and by him in his earlier works regarded as the only significance of branched spikes, wherever they may occur. It may be remarked in passing that certain cases of branching of the spike in *Ophioglossum* (Bower, *5*) are readily explained on the basis of splitting, and in one such case the anatomy of the leaf has been worked out (Holden, *11*) and found to be in accord with such a view.

There appears to be another group of cases of forked or divided spikes which can be most readily interpreted as branches of the regular monopodial order which are unusually remote from the other (higher) branches of the spike. The branches of a fertile spike are often distinctly alternate, and it can be readily seen how a strong basal branch may diverge at an unusually low level and give the appearance of an unequal fork. A large number of cases have been observed in which the smaller branch of a forking spike has every external appearance of being lateral in position, although it is evident that the stronger member of a pair of branches tends to straighten up and assume the appearance of a main axis. Several cases of branched spikes in *B. virginianum* have been observed in which the main stalk gives off a branch near its base, and at a point a half to one inch higher but on the opposite side of the stalk gives off a second branch. These triple spikes are most readily explained as cases of monopodial branching in which the two basal branches arise at a point lower than usual. Mr. Henry Mousley has very kindly sent me sketches of two specimens collected at Hatley, Quebec, each having three spikes, which appear to fall into this class. He has also been good enough to send a specimen in which one of the three branches of the spike undergoes a further division, giving the appearance of four branches of unequal sizes. It is a matter of common observation that in the various species of *Botrychium* the spike is broad and dense in some individuals, but skeleton-like or "stalky" in others, responding no doubt to differences in intensity of illumination. These stalky cases with long alternate branches merge imperceptibly into those which show what would at first sight be called cases of a double or triple spike. When the point of origin of two lateral branches is at about the same level, the true relation of the parts is still more disguised. *B. virginianum* is not the only species showing

this remote alternate branching but *B. Lunaria* L., *B. dissectum* Spreng., *B. neglectum* Wood afford other cases. What might be called multiple fertile spikes represent the normal condition in *B. lanceolatum* Angstr. and *B. ramosum* (Roth) Ascherson, for in these species several branches of the spike arise near its base and close together although plainly alternate, giving the corymbed or bunched appearance characteristic of these species.

The possibility is recognized that cases exist where it is difficult to say whether remote monopodial branching or chorisis is the better explanation of the facts. But the cases which have come under observation seem to render it desirable to distinguish between the normal monopodial method of branching and the splitting which appears to be a result of an external agency.

The third group of cases which has been styled "reversion" has already been figured by the writer (*8*). Examination of all available material indicates that replacement of a single fertile spike by a pair of spikes is practically restricted to the *Ternatum* section of the genus, and has been observed in *B. obliquum* Muhl., *B. dissectum* Spreng., *B. silaifolium* Presl, and in other species which have been at times distinguished by students of this puzzling group. It is not surprising to find that this group which is in a taxonomic jumble should present features suggesting evolutionary phases. The 98 abnormal specimens which have been examined by the writer fall readily into the following groups: (1) the fertile spike forking equally part way up its stalk (FIG. 1); (2) a pair of fertile spikes, of equal development, arising right and left at the same level (FIG. 2); (3) a pair of spikes as in the preceding group, but with an additional spike arising somewhat further up (FIG. 3); (4) a normal spike, and a smaller additional one inserted somewhat further up (FIG. 4); (5) a normal spike, and a pair of smaller ones inserted somewhat further up (FIG. 5).[1] Of these forms, most of which have already been pictured by the writer (*8*), the fourth one occurs more frequently than any of the others, and it probably includes two classes, namely, cases where the upper (smaller) spike represents one pinna and where it represents two fused pinnae, as shown by the single or double vascular supply. That is, the strand supplying such spike may arise from one edge of the C-shaped leaf trace, or a strand may

[1] A photograph of a plant of *B. dissectum* representing this type has been published by Weatherby (*17, pl. 1*).

arise from each edge of the trace. So far, only plants of the first class have been sectioned. The reasons for regarding abnormal plants of *B. obliquum* as supporting the theory of Roeper (*15*) as to the morphological nature of the fertile spike, namely, that this represents a fused pair of pinnae, the basal ones of the leaf, have been stated in an earlier paper (*8*) and supported by additional evidence from *B. lanuginosum* (*9*). The recent examination of herbarium specimens from a wide range has served to confirm the writer in his opinion, and lead him to regard the cases here figured as belonging to a different category from the branching spikes of *B. virginianum et al.* Whether the double and triple spiked specimens of *B. obliquum* are to be regarded as reversions in a strict genetic sense may be open to question, but it is sug-

FIGS. 1–5. Diagrams to illustrate the methods of insertion of the fertile spikes in abnormal specimens of *Botrychium obliquum* Muhl. *a*, *a'*, branches of the normal spike, representing the first and second pinnae. *b*, *b'*, supernumerary spikes, representing the third pinna or third and fourth pinnae.

gested that leaves showing such abnormal spikes are reminiscent of the stages passed through by the ancestors of the Ophioglossaceae.

It would be of interest to determine whether plants showing extra spikes continue to show the peculiarity in subsequent years. It would not be difficult to settle this question if a person were located near a station where many abnormal specimens are available. Something of this kind was undertaken by Mrs. Scoullar (*16*) who marked two plants, and obtained the following results: "*Botrychium matricariefolium:* June 15, 1904 (fertile), June 18, 1905 (two fruiting spikes), June 16, 1906 (sterile), June 21, 1907 (fertile). *Botrychium obliquum dissectum:* Aug. 20, 1904 (fertile), Sept. 1, 1905 (fertile), Sept. 8, 1906 (sterile), Sept. 10, 1907 (two fruiting spikes)." These observations

plainly indicate that the production of "two fruiting spikes" is not hereditary. But another method of inquiry is open, on account of the well-known habit of *Botrychium* of laying down the primordia of several leaves in the bud enclosed in the base of the petiole. If the feature of producing extra spikes were to become fixed in the constitution of an individual, it should be visible in the bud, say in a plant like FIG. 4, for in *B. obliquum* the spikes arise so far down on the rachis that it should be possible to distinguish them from sterile leaflets even in the embryonic stage. Four plants from the writer's slender stock of abnormal plants have been studied from this point of view by means of serial sections through the bud. In each of these cases a single fertile spike appears to arise in an altogether normal manner. This negative evidence is recorded, in the absence of a satisfactory investigation of the matter. In view of Goebel's observation (*10*) of the permanency of an abnormality at a station on the Ostsee, one might expect that the double-spiked character would persist.

2. The occurrence of sporangia on pinnae ordinarily sterile is widely distributed among the species of *Botrychium*, and was observed by some of the early students of the group, e.g., Roeper (*15*) who in 1859 figured an example in *B. Lunaria*. As to the extent of this feature, the sporangia may be present in small numbers on the margin of one or more pinnae, or a whole pinna, usually a basal one, may be transformed into a fertile segment, or in extreme cases the whole lamina may be converted into a fertile organ. Goebel (*10*) mentions a locality on the Ostsee where this condition has become constant. It is obvious that the cases where a basal pinna is fertile approach those abnormal specimens of *B. obliquum* in which there is a supernumerary small fertile spike inserted between the ordinary spike and the sterile segments of the leaf. Goebel (*l.c.*) has used the occurrence of fertile pinnae to support the view that the regular fertile spike is also produced from part of a foliage leaf, and his argument has been followed by others, including the writer.

3. More or less complete sterilization of the fertile spike, like the second abnormal feature, was early observed and figured. Roeper (*15*) figures a plant of *B. Lunaria* in which the fertile spike is entirely transformed into a green leaf-like organ. Cases of partial sterilization occur in various species; specimens of *B.*

cicutarium (Sav.) Sw., *B. neglectum* Wood, *B. silaifolium* Presl, and *B. obliquum* Muhl. illustrating this peculiarity have recently come under the notice of the writer. Malformations of this third order show the necessity for caution in reading too much of the supposed history of a genus into these abnormalities, for it must be remembered that it is a poor rule that will not work both ways. Bower (*6*) has uttered a warning on this matter, reminding us that *all* malformations must be taken into consideration in framing a theory. Fortunately the interpretation of the fertile spike in *Botrychium* does not rest solely on the evidence from monstrosities, but depends on the disposition of the vascular structures and on other collateral evidence. Since Bower has added his support to the idea of relating Ophioglossaceae to the true ferns rather than to the Lycopsida, we may consider that the consensus of opinion is in favor of regarding the fertile spike as an organ produced by the fusion of two basal pinnae of a fern leaf. The localization of spore-production in these basal pinnae implies derivation from ferns in which spore-production was not restricted to the basal part.

Localization of spore-production is in the majority of ferns apical rather than basal. A survey of common genera shows that when any part of the frond is sterile it is apt to be the basal region. Familiar examples are seen in the genus *Polystichum*. Whether the apical placement of sporangia is a light reaction ought to be open to determination by experiment. But it is easy to see how a relatively high location for sporangia would be of advantage in connection with dispersal of the spores, hence the teleological explanation readily occurs to one. Very few ferns have spore-production localized at the middle region of the leaf (e.g., *Osmunda Claytoniana* L.), and ferns in which the sporangia are situated on basal pinnae have these pinnae raised into a position favorable for dispersal of spores, e.g., *Anemia*, *Botrychium*.

It is convenient at this point to refer to certain peculiarities of the genus *Osmunda*. Although spore-production is fairly well localized in the apical region of the leaf in *O. regalis* and in the median region of *O. Claytoniana*, the oriental species *O. javanica* Blume may have its fertile part situated in the median, apical or even basal region, while some of the pinnae are intermediate between sterile and fertile, i.e., green pinnae show some sporangia

along one or both edges. This exceedingly variable species parallels *B. lanuginosum* (*3*, *7*, *9*), which has as a rule only one fertile pinna, occupying the position of second, third or higher pinna (up to the sixth at least), while in some specimens the fertile part is inserted at the base of the lamina[2] much as in *B. virginianum*. Inspection of a large series of specimens of *O. Claytoniana* shows that the number and location of fertile pinnae is subject to considerable variation; for instance, as few as two of the pinnae may be fertile, one or two of the fertile pinnae may stand opposite sterile pinnae, there may be no sterile pinnae below the group of fertile ones. The variation in extent of the terminal fertile region in *O. regalis* is of course familiar to all collectors. One specimen in the National Herbarium, collected in Miami, Florida, by Small and Nash, consists of a leaf which is entirely fertile, showing no green pinnules. Specimens exhibiting pinnules which are in part sterile and in part fertile are too common to merit more than passing mention. As for *O. cinnamomea* L., plants with leaves intermediate between sterile and fertile have sometimes been referred to as var. *frondosa* Gray. An inspection of forty-nine specimens of this "variety" shows six leaves sterile at the apex, thirty sterile at the base, ten sterile at both apex and base, and three transitional throughout. McLouth (*13*) reports the occurrence of "frondosa" stages in a swamp that had been burned over, to which cause he attributes the appearance of the intergrades. This explanation is rendered more probable by the experiment reported by Atkinson (*1*) who cut off the sterile leaves of *Onoclea sensibilis* L. as fast as they were produced (three times). In June and July these plants produced a large number of intermediate forms. Atkinson repeated the experiment with *O. Struthiopteris* Hoffmann, obtaining similar results. Dr. Kelley reports the finding of numerous intergrades in *O. sensibilis* in a pasture where the plants were browsed by cattle. The point of general import in these observations is the homology of fertile and sterile leaves and pinnae.

At least as far back as 1859 (Roeper, *15*) the significance of the genus *Anemia* in interpreting the condition in *Botrychium* was perceived. The two basal pinnae functioning as fertile leaflets and extending vertically are striking and suggestive objects. Equally suggestive are some of the abnormal specimens which oc-

[2] Reported in a letter from Professor D. H. Campbell.

casionally occur. Reference has been made elsewhere (Chrysler, 9) to cases showing only one fertile pinna; some doubt might arise as to whether this condition might occur through accidental loss or through abortion of one of the spikes. But in certain specimens of *A. adiantifolia* (L.) Sw. having the pinnae plainly arranged in alternate fashion it becomes clear that only the first (basal) pinna is fertile. Closely related to these cases are others in which a fertile pinna is paired with a sterile one at the base of the leaf, as is seen in FIG. 7, from a photograph kindly furnished by Dr. M. A. Howe of the New York Botanical Garden, from a specimen collected by Shafer in Camaguey, Cuba. Other specimens of this species have three of the lowermost pinnae fertile (e.g., National Herbarium no. 755693) and another specimen on the same sheet as the preceding shows the normal pair of fertile pinnae and a third pinna with three of its pinnules fertile and the remainder sterile. Dr. W. H. Maxon has very kindly called my attention to two remarkable specimens in which there are six fertile pinnae (National Herbarium numbers 372323, 520050, one of which is represented in FIG. 6). An examination of the sheets at the New York Botanical Garden brought to light two specimens collected in Jamaica by Underwood, each of which has four fertile pinnae. Another highly interesting specimen (*Underwood 3300*) is represented in FIG. 8, from a photograph kindly furnished by Dr. M. A. Howe, and it will be seen that almost an entire leaf is fertile. The common species *A. adiantifolia* is evidently a very variable one, as is also *A. cuneata* Kunze. An additional point of interest in the specimen shown in FIG. 8 is the resemblance of this abnormal form to those species of *Anemia* in which heterophylly is established, e.g., *A. aurita* Sw. and *A. millefolia* Gardner; in fact one might be tempted on this basis to establish a probable evolutionary line within the genus.

These abnormal forms in *Osmunda*, *Onoclea* and *Anemia* plainly point to the necessity of interpreting at least some of the cases of multiple spikes in *Botrychium* as additional fertile pinnae.

RUTGERS UNIVERSITY,
NEW BRUNSWICK, N. J.

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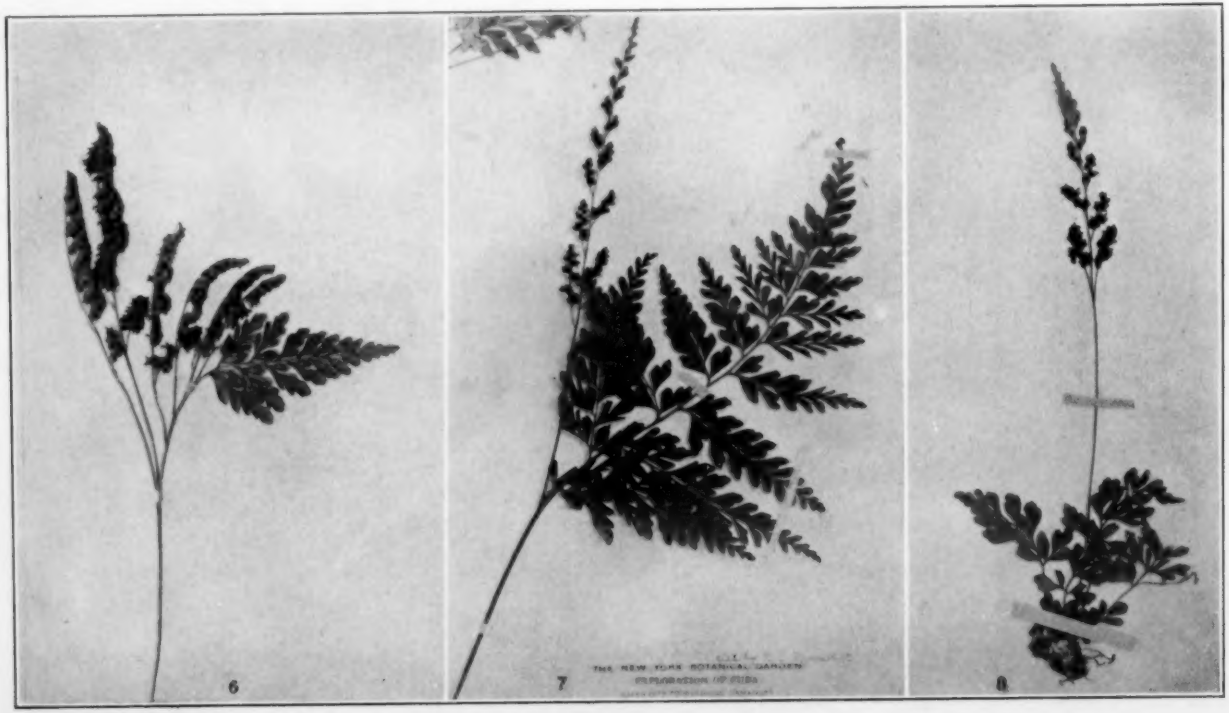
Explanation of plate 9

FIG. 6. ANEMIA ADIANTIFOLIA (L.) Sw.; specimen with four fertile pinnae in addition to the two normal ones (United States National Museum, no. 520050).

FIG. 7. ANEMIA ADIANTIFOLIA (L.) Sw.; specimen with one fertile pinna opposite a sterile pinna (New York Botanical Garden, *Shafer 1152*).

FIG. 8. ANEMIA ADIANTIFOLIA (L.) Sw.; specimen with one leaf almost wholly fertile (New York Botanical Garden, *Underwood 3300*).



ANEMIA ADIANTIFOLIA (L.) SWARTZ

UNIV. OF MICH.

Studies on the flora of northern South America—IX[1]

H. A. Gleason

MISCELLANEOUS NEW SPECIES FROM BRITISH GUIANA

Tetrapodenia n. gen. Malpighiaceae; arborescent, the young branches strongly flattened; stipules axillary, connate, erect; leaves opposite, petiolate, coriaceous, entire; flowers in minutely bracted, terminal racemes, on jointed pedicels; bracteoles 2, the lower glandular; calyx 10-glandular; petals 5, clawed, four essentially alike, the fifth much smaller, its blade bearing two pairs of latero-basal, stipitate, reniform glands; stamens 10, the five opposite the sepals the longer; filaments short, glabrous, somewhat triangular-dilated and barely connate at base; anthers elongate, the stout, simple, semicylindric or triangular-prismatic connectives truncate to broadly rounded at the apex; pollen-sacs 4, elongate, strictly parallel in the longer stamens, slightly divergent distally in two pairs in the shorter; ovary depressed-hemispheric, 3-celled, glabrous; styles 3, glabrous, bent near the tip at right angles and gradually tapering distally to the obliquely truncate terminal stigma; fruit indehiscent, 1-celled and 1-seeded by abortion, subellipsoid, the exocarp thick and woody, the endocarp chartaceous; seed ellipsoid, the small cotyledon partly enclosed by the large.

The name is combined from τέτρα, πούς, and ἀδήν, referring to the four stalked glands on the fifth petal.

Tetrapodenia glandifera n. sp. Tree 4–6 m. high; young branches strongly compressed, glabrous, later becoming terete and roughened by elongate lenticels; stipules triangular-subulate, erect, stiff, 6–8 mm. long, densely pubescent above; petioles 10–15 mm. long, glabrous, flattened or barely channeled above; leaf-blades stiff, coriaceous, dull green, elliptic-oblong, 10–17 cm. long, 4.5–8.5 cm. wide, abruptly acute or subacuminate, entire, broadly cuneate to obtuse or rounded at base, glabrous above, glabrous beneath (except under strong lens minutely lepidote) and biglandular at the base; veins and veinlets prominulous on both sides, conspicuously reticulate; racemes single or in threes, terminating the branches, the axis somewhat flattened and minutely puberulent, the bracts broadly ovate-triangular, 1–2 mm. long; pedicels 7–8 mm. long, glabrous, jointed in the middle, bearing on the lower segment two broadly ovate, amplexicaul bracteoles 1.5 mm. long, the lower of which bears a conspicuous gland; calyx-glands 10, cuneate-obovate, adnate to

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the summit of the pedicel; sepals triangular, acute or barely retuse, exceeding the glands by 1.3 mm.; petals dimorphic, clawed, the four larger with semiorbicular, subentire blade, cleft at base to the insertion of the claw, the fifth much smaller, obovate-oblong, with stout fleshy claw, the basal pair of glands 0.6 mm. in diameter, on stipes 0.5 mm. long, the distal pair half as large, on stipes one third as long; filaments flat, glabrous, 3 or 2 mm. long, dilated and barely connate at base; anthers stout 2–2.5 mm. long in bud, the simple connective somewhat surpassing the narrowly linear pollen-sacs; fruit smooth, 20–25 mm. long by 12–15 mm. in diameter, rounded at base, subacuminate to the blunt apex which is marked by 6 faint radial furrows.

Type, *La Cruz 3515*, collected at Amakura, Northwest District, British Guiana, 23–30 March 1923, and deposited in the herbarium of the New York Botanical Garden. *La Cruz 2176*, from the upper Mazaruni River, collected the preceding autumn, agrees with the type in all vegetative characters, except some small differences in texture due to age, and exhibits mature fruit and old flowers from which the petals have fallen. *La Cruz 2869*, with mature fruit, and *2043*, sterile, both from the Mazaruni region, differ from the first two in their larger, proportionately narrower, and more sharply acute leaves which are distinctly shining above. The fruit is precisely the same. The specific description is drawn entirely from the type, except that the length of the filaments is measured from the withered flowers of *2176*. Duplicates of all four numbers are to be found in the leading American herbaria.

Tetrapodenia is obviously closely related to *Glandonia* and *Burdachia*, two genera of the northern Amazonian forests which are still poorly known and have probably not been collected in recent years. The former is monotypic, but both flowers and fruit are known and were carefully described by Grisebach in the Flora Brasiliensis. The latter contains two species, but the flowers of only one are known. *Tetrapodenia* differs from *Glandonia* in its hirsute stipules, the glands on the lower surface of the leaf, the differentiated fifth petal, the unappendaged anther-sacs, the shape of the fruit, and the presence of two cotyledons. From *Burdachia prismatocarpa*, it is distinguished by the glabrous, depressed-hemispheric ovary, the simple blunt connectives, the character of the fifth petal, and the shape of the fruit. From *Burdachia sphaerocarpa*, the flowers of which are not known, it differs in its glabrous stipules and the shape of the fruit.

Tetrapodenia glandifera is represented in the herbarium of the Royal Botanic Garden at Kew by two collections by Jenman, *3779* and *6413*.

Combretum brunnescens n. sp. Shrubby vine, climbing 6 m.; stems glabrous, strongly furrowed and flattened above, becoming terete and barely striate in age, the upper internodes 5 cm. long; petioles stout, dark brown, 6–10 mm. long, angular, glabrous; leaf-blades coriaceous, olive-brown when dried, broadly elliptic-obovate, 70–85 mm. long, 43–58 mm. wide, obtuse to subrotund at base, entire, broadly rounded above and minutely apiculate, shining above, glabrous on both sides; lateral veins 5 or 6 pairs, lightly impressed above, prominent beneath, ascending at an angle of 60° and nearly straight, the veinlets obscure; panicles freely branched, terminal and from the upper axils, 10 cm. long; spikes spreading, 5–6 cm. long, the rachis strongly angled, glabrous; bracts subulate, puberulent, 0.5–1.1 mm. long; ovary sessile, linear-oblong, 1.1–1.3 mm. long, 0.4 mm. in diameter, obtusely 4-angled, glabrous or minutely villous; calyx campanulate, glabrous, conspicuously but minutely red-dotted, 1.7 mm. long, including the broadly triangular, acute teeth 0.4–0.5 mm. long, glabrous within; petals white, transversely elliptic, 1.4 mm. wide, 0.8 mm. long, glabrous, with a short claw 0.1 mm. long; stamens 8, inserted near the bottom of the calyx, the filaments white, glabrous, subulate, 4 mm. long, somewhat incurved at three-fourths of their length, the anthers obcordate, 0.4 mm. long and wide; disk a minute glabrous ring at the bottom of the calyx; style straight, white, subulate, 2.8 mm. long.

Type, *La Cruz 3566*, collected along the Amakura River, Northwest District, British Guiana, lat. about 8° 10′ N., long. about 60° W., 23–30 March 1923, and deposited in the herbarium of the New York Botanical Garden.

The type of *Combretum brunnescens* has been chosen arbitrarily from several specimens in the herbarium of the New York Botanical Garden, all collected in the same general region. Duplicates of most of them have been distributed to the larger American herbaria. These are *La Cruz 1094* and *1141* from the Pomeroon District, *3425*, *3585*, and *3713* from the Northwest District, *1947* from near Bartica, *4258* from Kamakusa, upper Mazaruni River, and *4460* from Kaieteur Falls, Potaro River. All but the last two of these are in flower and differ from the type only in minor details. In two from the Pomeroon District the largest leaves are only 6 cm. long; in all except *1947* and *3425* the leaves are more shining above; in *1141*, *1947*, *3585*, and *3713* the terminal apiculum of the leaf is more developed and

as much as 5 mm. long; in *1947* the largest leaves are 73 by 100 mm.; in *3425* the rhachis is sparsely villous. I have considered these discrepancies as representing merely the variability of the species and not worthy of taxonomic differentiation. Another sheet, *La Cruz 4460*, from Kaieteur Falls bears malformed fruits, and the leaves reach 103 by 140 mm. in size. *La Cruz 4258* is the only fruiting specimen: the leaves measure as much as 75 by 100 mm. and the fruit is ovoid, 18 mm. long by 11 mm. in diagonal diameter, strongly 4-winged, on a stipe 5 mm. long, and narrowed above to a subacute apex.

Through the key in Flora Brasiliensis, our species appears related to *C. Jacquinii* Griseb., a West Indian species properly known as *C. laxum* Jacq. It differs in the leaf-shape, in the fruit, and in the calyx glabrous within.

Combretum fusiforme n. sp. Stems terete, glabrous, the internodes 7–8 cm. long; petioles slender, glabrous, angular, 5 mm. long; leaf-blades thin but firm, olive-green, elliptic-oblong, 8–11 cm. long, 32–42 mm. wide, broadest slightly above the middle, rounded at the base, conspicuously acuminate, glabrous, somewhat shining above, dull green and minutely punctulate beneath, lateral veins about 7 pairs, arising at an angle of 80° and curved-ascending, veins and veinlets elevated on both surfaces and prominently reticulate; inflorescence and flowers lacking; fruit brown, fusiform, 40–48 mm. long, 8–11 mm. wide, acuminate to both ends, almost square in cross-section, sharply 4-angled, somewhat depressed along the center of each side, the cavity almost circular in cross-section.

Type, *La Cruz 4104*, collected at Kamakusa, upper Mazaruni River, British Guiana, long. about 59° 50′ W., 11–22 July 1923, and deposited in the herbarium of the New York Botanical Garden.

Combretum Sprucei Eichl. is the only other species known to me with fruit of similar size and proportions. It differs from *C. fusiforme* in having a sharply winged fruit with the sides projecting into the cavity.

Combretum fulgens n. sp. Stem shrubby, climbing, somewhat striate above and flattened at the nodes, terete when older, glabrous; petioles stout, thinly pubescent with simple brown hairs, 6–7 mm. long; leaf-blades firm or subcoriaceous, olive-green when dry, shining above, dull beneath, oblong to ovate-lanceolate, 11–12 cm. long, 40–52 mm. wide, broadest at or slightly below the middle, obtuse or subrotund at base, short-acuminate, glabrous on both sides, lateral veins 10–12 pairs,

lightly impressed above, elevated beneath, arising at an angle of 70° and gently curved-ascending, continuous almost to the margin, veinlets obscure above, faintly reticulate beneath; inflorescence of simple spikes in the upper axils, 5–8 cm. long, and sparingly branched terminal panicles 12 cm. long, the rhachis thinly pubescent with simple hairs; flowers not seen; fruit turbinate, 6–7 mm. long, 10–11 mm. in diagonal diameter, sharply 4-winged, rounded at base, truncate above, the lateral faces bearing 1 or 2 low irregular ridges in the distal half.

Type, *La Cruz 4129*, collected at Kamakusa, upper Mazaruni River, British Guiana, long. about 59° 50′ W., 11–22 July 1923, and deposited in the herbarium of the New York Botanical Garden. Specimens were distributed to various American herbaria under the name *Combretum nitidum* Spruce, to which it is closely related. In that species, as represented by *Spruce 1482* at Kew, the fruit is only half as large, not truncate at the apex, and without the conspicuous lateral ridges, the leaves are less shining, with lateral veins twice as far apart, and more acuminate, and the petioles are densely gray-lepidote.

Cybianthus Brownii n. sp. Shrubby, 3 m. tall; branches slender, irregularly angled, densely red-lepidote at the apex, sparsely so a few centimeters from the tip, and eventually glabrous; petioles slender, about 15 mm. long, finely and rather densely lepidote; leaf-blades bright green, thin, narrowly obovate to almost oblanceolate, abruptly subacuminate to an acute tip, entire, cuneate from above the middle to an acute base, sparsely black-punctate above, the lower surface more or less thickly red-dotted, closely beset with minute white glands, and sparsely black-punctate; veins elevated on both surfaces, finely reticulate; inflorescence racemose or subspicate, axillary, the staminate racemes 15–20 cm. long, rhachis sharply and irregularly angled, minutely and closely glandular-puberulent; bracts deciduous, subulate, 1.5–2 mm. long; pedicels stout, 1 mm. long; sepals firm, ovate, 1.5 mm. long, connate for one-third or more of their length, subacute, glabrous, conspicuously black-punctate; petals spreading, connate for more than half their length into a quadrangular or nearly square corolla, 4 mm. in diameter, the lobes broadly depressed-deltoid-ovate, obtuse or rounded, conspicuously punctate, especially at the margin; anthers inserted at one-third the length of the petals, strictly sessile, broadly flattened-ovoid, 0.6 mm. long and wide, with a large black gland on the back, dehiscing by two subintrorse terminal elliptical pores.

Type, *Gleason 159*, collected in dense upland forest, Tumatumari, British Guiana, 18 June to 8 July 1921, and deposited in the herbarium of the New York Botanical Garden. The

leaves on the type vary from 20 to 30 cm. long by 72 to 105 mm. wide. Here are referred also *Gleason 723*, from Butukari, on the Essequibo River (staminate); *Jenman 3977*, from the upper Demerara River (staminate); *La Cruz 2665*, from Malali, on the Demerara River (staminate); and *La Cruz 1601* and *1648*, from between the Demerara and the Berbice Rivers, near Wismar (fruiting). In the latter four sheets the leaf-blades are somewhat smaller than in the type, averaging 15–20 cm. long. The fruiting racemes are shorter than the staminate, mostly 4–6 cm. long; the mature berry is globular, 6 mm. in diameter, and densely verrucose-glandular.

Mez, in preparing his monograph, apparently did not examine *Jenman 3977*, the only specimen known to me which antedates his work. Our species, with its strongly punctate petals connate to well beyond the middle, is related, according to Mez' treatment, to *C. venezuelanus* Mez, but differs in its shorter pedicels, its remarkably broad petals, and in other details.

The species is named in honor of Mr. N. E. Brown, long a curator of the herbarium of the Royal Botanic Gardens at Kew, who has been of the greatest assistance in our studies of the plants of British Guiana.

Weigeltia sylvatica n. sp. Shrubby, 4 m. high; floriferous branches stout, irregularly angled, black-punctate and minutely fulvous-lepidote at the apex, glabrous below; petioles stout, glabrous, minutely rugulose, 12–15 mm. long; leaf-blades stiff, firm or coriaceous, reddish-brown when dried, elliptic-oblong to subobovate-oblong, 20 cm. long, 73–93 mm. wide, abruptly subacuminate to an acute tip, entire, acute and conspicuously inequilateral at base, glabrous on both sides, freely black-punctate along the midrib above, the lower surface very sparsely black-punctate, freely but minutely fulvous-lepidote, and densely and minutely white-punctate, the veins elevated and conspicuously reticulate on both sides; inflorescence axillary, virgately paniculate, the axis 4–11 cm. long, sharply angled, minutely puberulent with stout subcapitate hairs, the branches 3–15 mm. long, with 2–13 crowded flowers; bractlets subulate, 2 mm. long; pedicels stout, glabrous, 1 mm. long; flowers 4-merous; calyx 1.6 mm. long, the sepals connate for one-fifth of their length, the lobes oblong-triangular, 1.3 mm. long by 0.4–0.7 mm. wide, acute, entire, not punctate; petals 1.9 mm. long, connate for one-third of their length, the free portion ovate, 1.2 mm. wide, acute, entire, sparsely punctate; filaments inserted 0.5 mm. above the base of the corolla, truncate-triangular, 0.3 mm. long

and almost as broad; anthers dorsifix near the middle, depressed-ovate, 0.5 mm. long, 0.6 mm. wide, obtuse or truncate, not punctate, dehiscent by two longitudinal slits; ovary of the staminate flowers ovoid, glabrous.

Type, *Gleason 271*, collected in dense upland forest between Kangaruma and Potaro Landing, on the Potaro River above Tumatumari, British Guiana, 25–27 June 1921, and deposited in the herbarium of the New York Botanical Garden. According to the arrangement of species in Mez' monograph, *W. sylvatica* takes a position near *W. Schomburgkiana* Mez, from which it differs in the shape and texture of its leaves, the length of the pedicel, the pubescence of the rhachis, and the shape, size, margin, and punctation of the sepals and petals.

Bentham in 1876 described a new genus *Lissocarpa* of the family Styracaceae, based on Spruce's two collections, *3108* and *3504*, from the upper Rio Negro in northern Brazil. It is quite probable that these two specimens remained for a long time the only ones extant under that name, although the Kew herbarium contains two other old collections, one by Parker and the other *Jenman 4955*. The description was prepared with the usual detail of the Genera Plantarum, but may not have been entirely accurate, from lack of sufficient material. Gürke used Bentham's description of the genus in his presentation of the family in Die Natürlichen Pflanzenfamilien, although he probably did not see actual specimens, and supplied the plant with a specific name *Benthami*. Oliver published a plate and a page of description in 1895 (Hooker, Icones Plantarum, *pl. 2413*), in which he regrets that because of lack of material he was unable to ascertain satisfactorily the structure of the androecium. Miss Perkins, in her monograph of the family Styracaceae for Das Pflanzenreich, excluded *Lissocarpa*, but confessed that she was unable to suggest another place for it. Oliver, who admitted the genus to the Styracaceae, indicated its general resemblance to the Ebenaceae, apart from its wholly inferior ovary, a character found likewise in *Halesia* of the Styracaceae. The present writer believes the genus should remain where it was originally placed by Bentham.

Abundant material of the genus was collected by the writer in 1921, under the number *724*, from a single plant, a small tree perhaps twenty feet high. It was in full bloom, that is, the twigs were crowded with unopened flower-buds and the ground

beneath was carpeted with fallen corollas. No open corollas were observed on the tree. They are pure white, not "sordide lutei" as stated by Bentham and repeated by Oliver from their examination of dried material. Since then three other collections have been received from British Guiana.

Mr. N. E. Brown, on examining our collection, wrote: "A very distinct new species, with much larger flowers and leaves than *L. Benthami* has." Nevertheless, it was placed in our herbarium under Gürke's name, and it was not until the writer examined Spruce's plants personally, at Kew in 1924, that its specific distinctness was admitted. The two species may be distinguished as follows:

Leaves barely acuminate to a decidedly obtuse tip; midvein scarcely prominent above; lower leaf-surface distinctly dull-green or glaucous-brown, the veinlets obscure; exposed portion of corolla in mature buds 7 mm. long. *L. Benthami*

Leaves strongly acuminate to a sharply acute tip; midvein equally prominent on both sides; lower leaf-surface the same color as the upper, with very prominent, conspicuously reticulate veinlets; exposed portion of the corolla in mature buds 14 mm. long. *L. guianensis*

Lissocarpa guianensis n. sp. A small tree 6 m. or more high; leafy twigs finely roughened and mottled light and dark gray; petioles 5–7 mm. long; leaf-blades firm, dull-green, drying bronze-green, narrowly elliptic-oblong, 17–22(14–23) cm. long, 52–68 (41–92) mm. wide, strongly acuminate to a sharply acute tip, entire, cuneate to an acute (or occasionally subrotund) base, glabrous and shining with prominently elevated, strongly reticulate veins and veinlets on both sides; flowers in short, dense cymules in the axils or a few supra-axillary; pedicels 2–5 mm. long; bractlets 2, closely subtending the hypanthium, broadly rotund, somewhat scarious at the margin; flowers 5-merous; calyx and hypanthium narrowly obconic, 10–11 mm. long, the ovary wholly inferior, 4 mm. long, the calyx-tube thick and fleshy, 4 mm. long, the calyx-lobes broadly rotund, 2 mm. long, erect, rounded or somewhat retuse, minutely erose-denticulate; corolla salverform, pure white, drying almost black, fleshy, the tube obconic, 10 mm. long, the lobes elliptic, 16 mm. long by 8 mm. wide, obtuse, convolute in bud; stamens 8, inserted on the corolla-tube 3 mm. from its base, erect, included; filaments 1 mm. long; anthers linear, 4.7 mm. long, acuminate to a blunt tip, 2-celled, longitudinally dehiscent; coronal tube inserted on the corolla 6 mm. from its base, entire to the throat, distally cleft into 8, elliptical-oblong, sharply acute, projecting lobes 6 mm. long by 2 mm. wide; style slender below, thickened upward to the capitate stigma.

Type, *Gleason 724*, collected at Butukari, on the Essequibo

River, British Guiana, 20–21 July 1921, and deposited in the herbarium of the New York Botanical Garden. Other collections in the same herbarium are *Persaud 154*, from Hyde Park, near Georgetown, *La Cruz 3076*, from the upper Mazaruni River, and *La Cruz 3356*, from the Barima River, Northwest District. The dimensions stated in the description are taken from the type, the maximum and minimum sizes of the leaves are from the other three specimens.

It is difficult to contrast the flower-structure of the two species by reference to Oliver's plate, since he speaks of the scarcity of material for dissection, but the corolla-lobes of *L. guianensis* seem much longer in proportion to the tube, and also narrower and sharper than in *L. Benthami*, while the lobes of the coronal tube are narrower, sharper, and proportionately much longer. Our dissections answer one doubtful point raised by Oliver: the stamens are quite free from the coronal tube and inserted on the corolla-tube some distance below it.

Among the numerous interesting plants collected in British Guiana by J. S. De La Cruz are two sheets of the same species, illustrating a plant with such remarkable floral structure as to demand the erection of a new genus.

Barnhartia n. gen. Shrub or small tree; leaves alternate, petioled, simple, entire; flowers in simple or panicled raceme-like spikes, perigynous, somewhat zygomorphic; disk none; sepals 5, strongly imbricate, inserted on the summit of the hypanthium, distinct, pubescent; petals 5, valvate in the bud, clawed, inserted on the summit of the hypanthium, strongly hirsute within, 4 somewhat connate at base into two pairs, the fifth free and distinct; stamens 7 or 8, epipetalous, 5 opposite the petals and 2 or 3 alternate with them, each pair of petals bearing 2 opposite stamens and 1 alternate one, the odd petal bearing 1 opposite and sometimes 1 lateral alternate stamen; filaments short, flat, inserted near the summit of the claw; anthers flattened-ellipsoid, 2-celled, opening by a tangential cleft; ovary wholly superior, attached by a broad base, slightly flattened, 2-celled; ovule single in each cell, pendulous; style terminal, straight, pilose; stigma capitate, 2-lobed.

Barnhartia floribunda, n. sp. Stems minutely puberulent above, soon becoming glabrous, the internodes 1–2 cm. long; petioles nearly black, 5–10 mm. long, wrinkled or verrucose, glabrous; leaf-blades firm or subcoriaceous, bright green, narrowly elliptic-oblong, 10–12 cm. long, 3.5–4 cm. wide, subacuminate to an acute tip, entire, cuneate at base, glabrous, the veins and veinlets prominently elevated and conspicuously

reticulate on both sides; inflorescence of 1–3 simple or panicled raceme-like spikes from each of the upper axils, 2–5 cm. long, forming a terminal leafy panicle 10–15 cm. long, the axes thinly but densely gray-pubescent; bractlets subulate, 1.5 mm. long; flowers sessile, or on pedicels 1 mm. long; bracteoles broadly round-ovate, blunt, pubescent like the axis, 0.5 mm. long, closely subtending the hypanthium; hypanthium obconic, closely pubescent, nearly 1 mm. long; sepals thick, elliptic-oblong, 3.5–4 mm. long, densely pubescent or subtomentose; petals somewhat fleshy, linear-spatulate, 6.5 mm. long, the claw 3–3.2 mm. long by 0.5 mm. wide, orange-color, densely hirsute within, the blade maroon, 1.2 mm. wide, broadly rounded at the summit, hirsute within, the two pairs connate for half the length of the claw; filaments 0.5 mm. long, concealed in the pubescence of the claw; anthers 0.6 mm. long, the introrse valve soon shriveled and pendent; ovary 1 mm. in diameter, faintly 2-lobed; style straight, stout, 4–4.5 mm. long, pilose; stigma 0.7 mm. in diameter; fruit unknown.

Type, *La Cruz 2852*, collected at Kamakusa, upper Mazaruni River, British Guiana, 23–29 Nov. 1922, and deposited in the herbarium of the New York Botanical Garden. The type is in full bloom; a second sheet, *La Cruz 2727*, from Malali, on the Demerara River, was collected about a month earlier and is in bud. The two numbers differ only in unessential features, the leaves of the second reaching 13.5 cm. in length. Duplicates of both numbers are located in the principal American herbaria.

The arrangement of the petals in two loosely and partially connate pairs with a fifth one free is remarkable and is apparently the cause of the reduction in the number of the stamens from ten to seven or eight. All five petals are free and distinct at the level of the insertion of the short filaments. Each pair of petals bears three stamens, one at the center of each petal and a third on the margin of one of them toward the other member of the pair. There is no regularity in the location of the bistaminate petal. It may be either the posterior or the anterior of the two. The fifth or odd petal bears either a single central stamen, making a total of seven, or also a second lateral stamen, making eight for the whole flower. The three sinuses between the petals are somewhat wider than the width of the claw, and are obvious even in the unopened buds after dissection. The union of the paired petals is very weak and easily broken during dissection.

It is at once apparent that the three missing stamens, in the flowers with seven, are those which stand opposite the three

sinuses of the corolla. The two stamens of this set which are regularly present stand between the members of the pairs, but are always attached to the inner face of one petal at its margin. The eighth stamen, when present, has a similar marginal position on the fifth or odd petal. The slight connation of the paired petals is facilitated by their approximation on the margin of the hypanthium away from a normal position alternate with the sepals, and each of the pairs is exactly subtended by a sepal. The superior sepal subtends the sinus between the pairs of petals, while the fourth and fifth, or anterior, sepals subtend the sinuses between the pairs and the fifth petal and overlap behind it.

The complete epipetaly of the stamens and the tendency toward gamopetaly, or rather the tendency away from gamopetaly toward choripetaly, suggest at once the relationship of the genus to the Styracaceae. In that family, linear stamens and complete gamopetaly are the rule, but in the anomalous genus *Diclidanthera* the petals are only weakly gamopetalous and the anthers are precisely similar to those of *Barnhartia*. *Diclidanthera*, on the other hand, has a full complement of ten stamens, a salverform corolla, and a 5-celled ovary. Miss Perkins, in her monograph of Styracaceae for Das Pflanzenreich, rejected *Diclidanthera*, without suggesting a better position for it, and *Barnhartia*, which is certainly related, is additional evidence of their anomalous position.

The genus is dedicated to Dr. John Hendley Barnhart, whose extensive knowledge of botanical bibliography and biography has enabled him to render important service to his colleagues and his science.

Prestonia guianensis n. sp. Stems woody, twining, minutely verruculose, otherwise glabrous, the internodes 5–10 cm. long; stipules about 6 at each node, sharply triangular, 0.6 mm. long, subscarious; petioles 5–7 mm. long, glabrous or verrucose, channeled above; leaf-blades firm or subcoriaceous, ovate-oblong, 8–10 cm. long, 4–5 cm. wide, or the uppermost somewhat smaller; sharply and abruptly acuminate, entire, subrevolute, rounded at base, upper surface dark dull green, glabrous, lower surface brownish green, minutely scabrously roughened on the veins and veinlets; venation lightly reticulate above, strongly reticulate beneath, midvein and primary veins shallowly impressed above, the veinlets plane, all very prominently elevated beneath; primary veins about 8 pairs, abruptly and arcuately

anastomosing near the margin; peduncles axillary, 3–4 cm. long, glabrous; pedicels (and rhachis) minutely puberulent, 10–15 mm. long, in a crowded raceme, subtended by 2 or 3 minute, subulate, pale bracts; sepals ascending, elliptic-ovate, 9 mm. long, 4 mm. wide, acute, glabrous, subprominently longitudinally veined, each with an interior, basal, broadly triangular, subacute, glabrous scale almost equaling the disk; corolla-tube cylindric, stout, 13 mm. long, glabrous without, softly villous within on the upper 4 mm., conspicuously thickened into a cartilaginous ring at the throat, unappendaged; corolla-limb spreading, the lobes 12 mm. long, broadly rounded at apex, glabrous, a basal central ovate-elliptic portion 9 mm. long, acute, reticulately veined, and comparatively firm, the distal portion very thinly membranous; filaments 3 mm. long, the basal portion filiform and densely villous, the distal portion nearly glabrous and obtriangularly flattened; anthers linear-subulate, cohering in a cone, 3.5 mm. long over all, protruding 2 mm. from the corolla-tube, polliniferous in the distal half, minutely pubescent dorsally on the central half, united to the stigma by a narrow introrse ventral ring at the center, prolonged below at the sides into linear-subulate caudae 0.7 mm. long and at the middle into a triangular-acuminate, scarious membrane of the same length; style minutely subclavate at apex, slightly thickened toward the base; disk fleshy, 1.5 mm. long, 5-lobed to the base, the lobes equaling the ovary, glabrous, ovoid, truncate and minutely 2–4-crenulate at apex; ovaries ovoid, subacute, glabrous; fruit not seen.

Type, *La Cruz 3097*, collected on the Pomeroon River, Pomeroon District, British Guiana, and deposited in the herbarium of the New York Botanical Garden. Duplicates are located in the Gray Herbarium and the United States National Herbarium. It was noted by the collector as climbing four feet high; the corolla is apparently yellow. There can be no doubt of its position in the genus *Prestonia*, although the small scale-like appendages at the throat of the corolla are missing. I know of no other species in the genus to which it bears a close similarity.

Odontonema macrophyllum n. sp. Stems shrubby, 1–2 m. tall, leafless below, obscurely angled above, glabrous or nearly so; leaf-blades bright green, thin and membranous, obovate-elliptic, the principal ones 20–23 cm. long by 7–9 cm. wide, sharply acuminate into a slender tip, entire, cuneate from near the middle to a narrowly alate, pubescent petiole 2–4 cm. long, minutely and sparsely puberulent on the upper surface with appressed evanescent hairs 0.1–0.2 mm. long (and in no. 213 also with scattered, flat, crooked hairs 1.5–2 mm. long), pubescent below

with flat, crooked hairs 1.5–2 mm. long scattered over the surface and crowded along the principal veins; racemes lax, 25–30 cm. long, floriferous on the upper half, the axis, bracts, pedicels, and calyx closely pubescent with spreading, purplish, conspicuously septate hairs 0.5 mm. long; bracts linear-subulate, 5 mm. long; pedicels single and opposite or in opposite pairs, gradually elongating at anthesis to 7 mm.; calyx-tube 1.2 mm. long; sepals linear-triangular, 8 mm. long; corolla red, the tube minutely puberulent, 4 cm. long, the lobes 5 mm. long, obtuse, ovate.

Type, *Gleason 213*, collected in an Indian clearing at Kangaruma, on the Potaro River above Tumatumari, British Guiana, 25–27 June 1921, and deposited in the herbarium of the New York Botanical Garden. A second sheet, *Gleason 7*, from wet lowland forest at Tumatumari, 18–20 June 1921, lacks the longer hairs on the upper leaf-surface.

The species is closely related to *Odontonema Schomburgkianum* (Nees) Kuntze (*Thyrsacanthus Schomburgkianus* Nees), the original material of which has been examined in the Kew Herbarium. There the leaves are distinctly smaller, thicker, narrower, and more gradually cuneate to the base, the larger ones averaging 12–17 cm. long by 3.5–4.5 cm. wide, the stem is conspicuously angled, the raceme less pubescent, and the narrower sepals are only 4–5 mm. long. Recent collections of Nees' species from British Guiana are *Gleason 699*, *La Cruz 2989*, and *La Cruz 137*.

Additions to the genus Lycianthes—A correction

In the title of my article on the genus *Lycianthes* in the April number of the BULLETIN (**53**: 209–213) I omitted placing the name Dunal in parentheses, followed by that of Hassler, who elevated *Lycianthes* to generic rank. I should also have said that most of the later described species, rather than the whole of *Brachistus*, were transferred to *Lycianthes* by Bitter.

I find that the name *Lycianthes ferruginea* is preoccupied. My *Bassovia ferruginea* will therefore require renaming, and I substitute the name **Lycianthes rufinervia.**

H. H. RUSBY.

Contributions to the flora of Long Island, New York
Fourth paper[1]

WILLIAM C. FERGUSON

The plants listed below represent species collected during 1925 that, in the writer's experience, are from very rare to uncommon. In addition, localities are given for species not uncommon, where the records furnished by Mr. Norman Taylor, of the Brooklyn Botanic Garden, show one, two, or possibly three localities. All plants except three or four of the more common ones were collected by the writer from all the localities named, and specimens from each locality are in his herbarium. With one or two exceptions duplicates of all the rarer plants have been deposited in public herbaria. This is also true of the rarer plants listed in former papers. All critical specimens have been reviewed by professional botanists specializing in such plants.

The writer acknowledges with grateful appreciation this generous aid which adds so much to the permanent value of what is recorded.

Mrs. Agnes Chase has reviewed all the grasses.

Mr. Kenneth K. Mackenzie has reviewed *Carex*.

Professor T. G. Yuncker has reviewed *Cuscuta*.

Professor M. L. Fernald, and other authorities, whose names appear with the plants determined or corroborated by them, have reviewed many specimens.

POLYPODIACEAE

DRYOPTERIS HEXAGONOPTERA (Michx.) C.Ch. Hilly, rich woods; uncommon. Millneck; North Deer Park; Port Washington; Queens; Plattsdale; Bayside; Southold.

LYCOPODIACEAE

LYCOPODIUM LUCIDULUM Michx. Wet and damp rich and mostly hilly woods; rare. Plattsdale; Wyandanch; Farmingdale; Smithtown; Millneck; Cold Spring Harbor.

SPARGANIACEAE

SPARGANIUM EURYCARPUM Engelm. Swamps; rare. Montauk (two or more stations); Winfield.

[1] Previous papers in this series appeared in Torreya **22**: 43–49. 1922; Bull. Torrey Club **51**: 177–201. 1924; Bull. Torrey Club **52**: 133–136. 1925.

VALLISNERIACEAE

PHILOTRIA NUTTALLII (Planch.) Rydb. Determined by P. A. Rydberg. Streams and ponds; uncommon. Cold Spring Harbor; Millneck; Woodside; Mattituck.

GRAMINEAE

SPARTINA PATENS CAESPITOSA (A. A. Eaton) Hitch. Massapequa: salt marsh. "Larger than type; not caespitose, shows short rhizome"—Mrs. Chase.

STIPA AVENACEA L. Dry oak woods; rare. Hither woods, Montauk.

SPOROBOLUS CRYPTANDRUS (Torr.) A. Gray.[2] Very rare. Bayville: dry sandy ridge just back of sea beach.

MUHLENBERGIA SOBOLIFERA (Muhl.) Trin. Rich hilly woods: Queens. Very rare. Only one colony of 3 or 4 plants. The writer can find no previous record for Long Island.

BRACHYELYTRUM ERECTUM (Schreb.) Beauv. Hilly rich woods; uncommon. Millneck; Smithtown; Port Washington; Queens.

SPHENOPHOLIS OBTUSATA (Michx.) Scribn. Meadow near salt marsh; rare. Merrick.

PANICUM LONGIFOLIUM Torr. Open swamp, bogs, and damp meadows; not uncommon. Bridgehampton; Manorville; Yaphank; Wyandanch; Rockville Centre; Hempstead.

PANICUM AMARUM Ell. Sea beaches; rare, but locally abundant at Eaton's Neck. Southold; Point O'Woods; Wading River; Bayville. In the first three localities the plants were few and scattered; at Bayville there were a few dense colonies of very large plants; at Eaton's Neck, back of the sand dunes, there were thousands of plants growing for a long distance.

PANICUM BICKNELLII Nash. Open sand, dry oak woods, and pine barrens; uncommon. Smithtown; Wantagh; Massapequa; Ronkonkoma; Hempstead Reservoir. Where the writer has found this plant it was represented by a single clump, except at the Hempstead Reservoir, where there is a colony of perhaps a dozen.

PANICUM COMMUTATUM Schult. Very rare. Laurelton, wet sand, edge of marsh; Cypress Hills, dry hilly woods.

PANICUM WRIGHTIANUM Scribn. Wet sandy shores, and damp grassy meadows; very rare. Sag Harbor, Long Pond; Bridgehampton, Poxabogue Pond.

PANICUM LATIFOLIUM L. Dry rich woods, and open scrub; not uncommon. Port Washington; Orient; Cypress Hills; Queens; Kew Gardens; Rockville Centre; Richmond Hill; Plattsdale; Forest Park.

CYPERACEAE

ELEOCHARIS ROBBINSII Oakes. Shallow water, boggy shores, and bogs; uncommon. Watermill; Bridgehampton; Smithtown; Ronkonkoma; Sag Harbor.

SCLERIA RETICULARIS Poir. Wet sandy shores; rare. Bridgehampton, Poxabogue Pond; Sag Harbor, Long Pond.

PSILOCARYA NITENS (Vahl) Wood. Wet sandy shore; very rare. Sag Harbor, Long Pond.

CAREX SHRIVERI Britton. Swampy woods; very rare. Woodside.

[2] Reported by Homer D. House. Annotated list of the ferns and flowering plants of New York State. 1924.

CAREX WILLDENOVII Schk. Very rare. Greenport, open dry spot in swampy woods. (Previously reported from same locality by Roy Latham.)

CAREX PALLESCENS L. Bog; rare. Flushing. Only one clump seen.

CAREX COLLINSII Nutt. Very shady thickets in wet sphagnum; uncommon. Smithtown; Massapequa; Merrick; Wyandanch, two stations, one in hills and one in level pine barrens; Central Islip, in pine barrens.

CAREX ANCEPS Muhl. Rich hilly woods; not uncommon. Queens; Deer Park; Richmond Hill; Millneck; Kew Gardens; Roslyn; Cutchogue; Peconic. (The last two collected by Roy Latham.)

CAREX LAEVI-VAGINATA (Küken.) Mackenzie. Swamps; not at all uncommon on Long Island, about as plentiful as *Carex stipata*, and found in the same situations. The writer has more than once found them a few feet apart. Flushing; Meadowbrook; Setauket; Montauk; Rockville Centre; Millneck; Lakeview; Farmingdale; Wading River; Wyandanch.

JUNCACEAE

JUNCUS ARISTULATUS Michx. Borders of bogs, swamps and marshes; rare. Mattituck; Sag Harbor, Long Pond (2 stations). Determined by F. V. Coville.

JUNCUS ARTICULATUS L. Bogs, swamps, wet borders streams and ponds; uncommon. Seaford; Watermill; Montauk; Point O'Woods.

HAEMODORACEAE

GYROTHECA TINCTORIA (Walt.) Salisb. Wet sandy shores; very rare. Sag Harbor, Long Pond.

POLYGONACEAE

TINIARIA CILINODIS (Michx.) Small. Swampy open hilly woods; very rare. Cypress Hills, large colony. Determined by J. K. Small.

CHENOPODIACEAE

ATRIPLEX PATULA L. Grassy roadside; rare. Hempstead. Determined by Paul C. Standley, who states: "a form of *Atriplex patula*, which in turn may be a variety of *Atriplex hastata*."

DROSERACEAE

DROSERA FILIFORMIS Raf. Wet sandy shores and sandy bogs; uncommon. Sag Harbor, Long Pond; Bridgehampton; Montauk, Fort Pond; Manorville; Wading River, Long Pond.

FABACEAE

MEIBOMIA LAEVIGATA (Nutt.) Kuntze. Dry hilly oak woods; very rare. Sag Harbor, Long Pond, one small colony. Determined by J. K. Small.

FALCATA PITCHERI (T. & G.) Kuntze. Swamps and moist thickets; rare. Cold Spring Harbor; Flushing.

ELATINACEAE

ELATINE MINIMA (Nutt.) Fish. & Mey. Wet shores; uncommon. Determinations by M. L. Fernald. Montauk; Southold; Laurel. (Last two collected by Roy Latham.)

VIOLACEAE

VIOLA EMARGINATA Le Conte. Dry oaks woods, plains, and pine barrens; uncommon. Hempstead Plains, at Hicksville and in Isle of Pines; Massapequa; Ronkonkoma; Plattsdale; Brentwood; Wyandanch; Central Islip. Mostly determined by Ezra Brainerd. (Intergrades with *V. sagittata* and *V. fimbriatula*.)

ARALIACEAE

ARALIA RACEMOSA L. Hilly rich woods; uncommon. Plattsdale; Albertson; Queens; Wyandanch; Rosyln; Cold Spring Harbor.

ARALIA HISPIDA Vent. Dry or wet sandy ground; uncommon. Cutchogue; Flanders.

AMMIACEAE

SANICULA GREGARIA Bicknell. Hilly rich woods; uncommon. Cold Spring Harbor; Richmond Hill; Millneek; Bayside. *Sanicula marylandica* and *Sanicula canadensis* are both widespread and common on Long Island.

WASHINGTONIA CLAYTONI (Michx.) Britton. Hilly rich woods. Not nearly as common as *Washingtonia longistylis*, and usually much smaller; plants one-half the size or but little more with rare exceptions.

HYDROCOTYLE AMERICANA L. Wet places in rich woods; uncommon. Millneck; East Hempstead; Plattsdale.

HYDROCOTYLE UMBELLATA L. Swamps and wet shores, mostly in water; rare. Montauk, Great Pond and Fort Pond; Sag Harbor, Long Pond; seen at Watermill.

OXYPOLIS RIGIDIOR (L.) Raf. Swamps; not uncommon. Massapequa; Valley Stream; East Meadowbrook.

MONOTROPACEAE

HYPOPITYS AMERICANA (DC.) Small. Very rare. Very wet rich woods, south of Meadowbrook, one small colony. Determination by J. K. Small. The writer can find no previous record for Long Island.

HYPOPITYS LANUGINOSA (Michx.) Nutt. Dry hilly oak woods. Kings Park; Smithtown; Montauk, Hither Woods. Determinations by J. K. Small.

HYPOPITYS INSIGNATA Bicknell. Dry oak woods; not uncommon. Smithtown; Ronkonkoma; Sag Harbor; East Hempstead; Deer Park; Pinelawn; Central Park; Wyandanch. This species matures about six weeks later than the others.

VACCINIACEAE

VACCINIUM CAESARIENSE Mackenzie. Swamp; rare. Ronkonkoma. Determination confirmed by P. C. Standley.

OXYCOCCUS OXYCOCCUS (L.) MacM.[3] Sphagnum bog, Ronkonkoma. Very rare.

[3] Norman Taylor, of the Brooklyn Botanic Garden, in a letter to the writer dated September 28, 1925, states: "Your collection of the small-fruited cranberry is the first to come from Long Island. E. S. Miller reported it from Wading River in the Bulletin of the Torrey Club **7:** 18. 1880 and **10:** 120. 1883. But his herbarium shows no specimens from that place."

It is of interest to record that in this same bog *Lycopodium carolinianum* was discovered by the writer a few years ago, not before known north of the New Jersey pine barrens, while *Oxycoccus Oxycoccus* is a plant of more northern or cooler climate than Long Island.

GENTIANACEAE

BARTONIA PANICULATA (Michx.) Robinson.[4] Damp or wet open places, and woods; widely distributed, but nowhere common. From some localities the writer found but one or two plants very variable. Determinations confirmed by M. L. Fernald, who writes: "*B. paniculata* beheaves with you much as it does in eastern Massachusetts, but none of the specimens are so extreme as in Nova Scotia and Newfoundland." Montauk Point; Hempstead; Smithtown; Ronkonkoma; Flushing; Wyandanch; South Meadowbrook; Cold Spring Harbor; Millneck; Merrick; North Bellmore; Rockville Centre; Roslyn; Valley Stream. Some of the above plants were purplish-colored, but with no constant relation to any definite form. The plant found at Hempstead was found growing associated with *Bartonia virginica*, and both species were equally purplish-colored.

CUSCUTACEAE

On shrubs and herbs in swamps, bogs, swampy woods, and borders of ponds and streams. Determinations by T. G. Yuncker.

CUSCUTA POLYGONORUM Engelm. Very rare. Plattsdale, two colonies; Queens, woods. The writer can find no previous record for New York State.

CUSCUTA CORYLI Engelm. Sag Harbor. Very rare.

CUSCUTA COMPACTA Juss. Not uncommon. Valley Stream; South Meadowbrook; Laurel; Central Islip; Wyandanch; Smithtown; Flushing; Rosyln.

CUSCUTA GRONOVII LATIFOLIA Engelm.[5] Not uncommon. Sag Harbor; Valley Stream; Millneck; Watermill; South Meadowbrook; Montauk; Flushing.

CUSCUTA GRONOVII VULGIVAGA Engelm. Not uncommon. Queens; Valley Stream; Cold Spring Harbor.

LABIATAE

CLINPODIUM VULGARE L. Hilly rich woods; rare. Plattsdale; Wyandanch.

SCHROPHULARIACEAE

GRATIOLA NEGLECTA Torr.[6] (*Gratiola virginica* of Manuals). Wet borders of woods, swamps and ponds; uncommon. Flushing; Millneck; Plattsdale; Massapequa.

ILYSANTHES DUBIA (L.) Barnhart.[6] Swamps; rare. Plattsdale; Massapequa.

[4] Fernald, M. L. Rhodora **23:** 149, 153, 157, 286–288. 1921.
Bicknell, E. P. Bull. Torrey Club **42:** 32–33. 1915.

[5] In letter of October 16, 1925 to the writer, Professor Yuncker states: "It is often difficult to distinguish variety *latifolia* from *vulgivaga* of *Gronovii*. *Latifolia* has calyx lobes which reach, or almost reach, the corolla sinuses. The flowers are usually shorter than *vulgivaga* which has the calyx about half as long or less as the corolla tube. However, these two varieties merge one into the other so that it is difficult to keep them apart. In their extremes they are readily separable, but intergrading specimens are common."

[6] Pennell, F. W. Torreya **19:** 143–152. 1919.

ILYSANTHES INAEQUALIS (Walt.) Pennell.[6] Swamps; not uncommon. Valley Stream; Plattsdale; Montauk; Cypress Hills; Calverton; Sweezytown; Central Islip, pine barrens.

LENTIBULARIACEAE

SETISCAPELLA CLEISTOGAMA (A. Gray) Barnhart. Wet sandy borders of ponds and streams, sandy swamps; rare. Sag Harbor, Long Pond; Central Islip, pine barren bog. In the last named locality the plant was growing where, earlier in the season in former years, *Setiscapella subulata* was collected by the writer in full flower. The writer had noted this same association at Long Pond, Wading River. For his comments on this, and for that of other field observers see Bull. Torrey Club **51:** 198. 1924.

OROBANCHACEAE

THALESIA UNIFLORA (L.) Britton. Woods. Hempstead Reservoir; Plattsdale.

PLANTAGINACEAE

PLANTAGO JUNCOIDES DECIPIENS (Barneoud) Fernald.[7] Very rare. Grassy cliffs at sea beach, Montauk Point. Determined by M. L. Fernald.

PLANTAGO OLIGANTHOS Roem. & Schultes.[8] Salt marshes; not uncommon. Determined by M. L. Fernald. Cutchogue; Napeague; Freeport; Cold Spring Harbor.

RUBIACEAE

DIODIA TERES Walt. Open dry sand; not uncommon. Hempstead Plains, Garden City; Valley Stream; Springfield; Jamaica; Aqueduct; Sag Harbor.

LOBELIACEAE

LOBELIA DORTMANNA L. In shallow water; very rare in distribution, but plentiful where found. Watermill, Lake Nowedonah; North Sea, Big Fresh Pond.

COMPOSITAE

HELENIUM AUTUMNALE L. Swamps; rare. Valley Stream.

EUPATORIUM PUBESCENS Muhl. Dry meadow; very rare. Long Pond, Sag Harbor. Determined by J. K. Small.

SOLIDAGO SPECIOSA Nutt. Open field and dry open woods. Not uncommon but mostly in very small colonies, sometimes but two or three plants; locally abundant at Port Washington. Wyandanch; Southold; Albertson; Montauk; Orient; Millneck; Massapequa.

[7] Fernald, M. L. The maritime plantains of North America. Rhodora **27:** 93–104. 1925.

[8] According to the writer's understanding both of the maritime plantains listed above have been combined as one species in the following works:

Britton & Brown's Illustrated Flora	—*Plantago maritima* L.
Gray's Manual. 7th ed.	—*Plantago decipiens* Barneoud
House's Annotated List of the Ferns and Flowering Plants of New York State	—*Plantago gibbosa* Raf.

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